# VARIATION IN EPIPHYTIC BRYOPHYTE COMPOSITION WITHIN AND BETWEEN ASH TREES AT TUNGESVIK, ETNE, W. NORWAY

Master of Science Thesis in Ecology and Evolution

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# ABSTRACT

The epiphytic bryophyte composition between and within 73 ash trees (minimum stem diameter at breast height 20 cm) at Tungesvik, Etne, West Norway was investigated. The main aim of the study was to investigate patterns of variation in epiphytic bryophyte species composition on ash (*Fraxinus excelsior*) by a multivariate (ordination) approach. The importance of pollarding for the epiphytic bryophyte composition was also investigated. Trees were selected randomly from all realized combinations of three strata: elevation above sea; tree diameter; and pollarding or non-pollarding. Each tree was divided into height zones and sectors, in combinations of which bryophytes and environmental variables were recorded separately to address variation within trees. Pollarded trees were divided into five height zones – basis, stem, top, pollarded crown and pollarded branches – while non-pollarded trees were divided into three height zones – basis, lower stem and upper stem.

The ordination analysis revealed a main gradient in bryophyte species composition that reflected variation on two spatial scales, between as well as within trees. The most important factors making up the underlying complex gradient were bryophyte cover, tree circumference and height zones. On the scale of variation between trees, the main gradient described variation from trees with small diameter and high bryophyte cover to trees with larger diameter and lower moss cover. A tendency for decreasing bryophyte cover with increasing tree diameter may be explained by the age-aspect of the tree's circumference, more specifically, that young trees with small circumference (which are not included in this study) are relatively rapidly colonised by a handful of species with good dispersal and establishment ability. In later phases of succession, the species richness increases and the species composition changes as the bark undergo structural (and chemical) changes.

On the scale of variation within trees, the main gradient in bryophyte species composition was related to tree height zones, running from the basis of the tree with high moss cover and low (naked) bark and lichen cover to higher height zones with lower moss cover and higher cover of naked bark and lichen cover. This pattern may be explained by shifts in the slope between the zones, which affects the species' ability to hold on to a more vertical substrate, and by responses to a water availability gradient: with increasing height on the trunk, environments get drier due to greater wind speeds and turbulence and reduced influence by evaporation from the ground.

The difference in species composition between pollarded and non-pollarded trees was shown to be small, although there was a small general trend for the pollarded zones to have lower bryophyte cover than non-pollarded trees was observed. This indicates that pollarding *as such* that is not important for bryophyte species composition, except for the tendency for pollarded trees to be larger.

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# INTRODUCTION

Bryophyte diversity is an essential part of the overall diversity in forests. This is especially the case for old-growth deciduous forests which are considered among the most species-rich nature types. A total of 220 species of bryophytes are listed as dependent on these old forests in Norway (Frisvoll 1996). Along the west coast of Norway there are several old-growth deciduous forest stands of which many have been used for fodder harvesting for several decades (Austad and Skogen 1990). These coastal regions are strongly influenced by Atlantic winds and the Gulf Stream, providing a climate that is warmer and wetter than expected at these latitudes (Moen et al. 1999). The wet and mild climate is especially important for bryophytes growing on dry substrates such as tree bark (Potzger 1939, Ingerpuu et al. 2007). 'Rich-bark' (Du Rietz 1945) deciduous trees like *Fraxinus excelsior* (ash) are especially rich in bryophyte species because they provide a habitat with significantly higher pH and higher availability of nutrient (*e.g.*, nitrogen) than other tree species (Nordén 1991). These base-rich trees, like ash, have been suggested to be the one of the most important factors affecting species composition and diversity of lichens and bryophytes (Barkman 1958, Weibull and Rydin 2005). Trees in a forest provide a dynamic island landscape of patchy habitats, constituting a metacommunity for the epiphytic mosses. Tree boles are dynamic patch-type habitats which are bound to emerge, grow and fall. In order to be successful, epiphytic species have to be able to cope with the dynamics of the substrate, which puts demands on dispersal efficiency, ability to establish on vertical substrates, and rapid local spread (Smith 1982). Several environmental factors have been shown to influence the distribution of epiphytic bryophytes, among others the size or age of host tree; position along the trunk; light levels; exposition; and microclimate (Barkman 1958, Kuusinen and Penttinen 1999, Hedenas et al. 2003). The relative importance of these factors seem to vary from study to study, and no general agreement have been reached about the relative importance of environmental factors, or if this importance varies regionally and locally (Gustafsson and Eriksson 1995, Perpetua et al. 2005, Mežaka et al. 2008). I Norway the bryophyte diversity is over 1/3 of the total diversity of all land plants, but still the research, compared to vascular plants, is modest. There are especially few previous systematical investigations of epiphytic bryophyte vegetation in Norway (Moe and Botnen 1997, Heegaard and Hangelbroek 1999, Moe and Botnen 2000), although this has been more investigated in Sweden (Hedenås et al. 2003, Fritz et al. 2009, Löbel and Rydin 2009) and also in other countries (McGee and Kimmerer 2004, Király and Ódor 2010, Rambo 2010).

Previous investigations on species distribution and occurrence patterns for epiphytic bryophytes along the west coast of Norway have mainly been carried out in pollarded forests (Austad and Skogen 1988, Austad and Skogen 1990, Moe and Botnen 1997, Moe and Botnen 2000). Pollarding is the process by which tree branches are cut

2–3 meters above ground. The cut-off was used as supplementary animal fodder in winter (Austad and Skogen 1988). Pollarding was common in deciduous forests in western Norway, where the practice of pollarding can be traced back to the Iron Age (Austad and Skogen 1988). In this region, pollarding declined throughout the 20th century (Austad and Skogen 1988). Today pollarding for fodder harvesting has completely ceased, and formerly pollarded forests either develop into natural deciduous forests (Moe and Botnen 2000) or are replaced by planted Norway spruce (*Picea abies*) or other tree species (Austad and Skogen 1988). However, there are still many remaining pollarded trees in these forests, because of tree longevity. One example of a deciduous forest rich in formerly pollarded trees is the Tungesvikstranda forest in Etne municipality (Hordaland County), in which trees were pollarded for several centuries (Brekke 2001) until pollarding ceased about 20–30 years ago. Pollarded trees can live for several hundreds of years (Timdal et al. 2010) and the age of trees have affected the distribution of bryophyte species and variation in bryophyte richness as such. Former studies have shown that pollarded trees tend to be rich in epiphyte species (Rose 1992, Nilsson et al. 1994), although no investigations have been made to assess if pollarded trees have an innate effect on epiphytic species diversity, or if old non-pollarded trees can contribute similar epiphyte richness. Previous studies have stated that qualities brought by pollarding that enhance epiphytic diversity are, *e.g.,* reduced canopy cover and increased diameter(Austad and Skogen 1990, Moe and Botnen 1997), although it is not yet known if the distribution and occurrences of bryophytes are significantly different on pollarded trees than on non-pollarded trees.

The main aim of this study is to investigate patterns of variation in epiphytic bryophyte distribution and species composition on ash (*Fraxinus excelsior*) at Tungesvikstranda (Skånevik, Etne, Hordaland, West-Norway), by a multivariate (ordination) approach. Scale of variation (*e.g.,* between- and within-trees) is particularly addressed. As a secondary aim, the importance of pollarding for the epiphytic bryophyte composition is assessed.

# MATERIAL AND METHODS

## THE STUDY AREA

The study area, Tungesvikstranden, is located in the municipality Etne, south in Hordaland County, West-Norway (see Figure 1). Tungesvikstranden is a deciduous woodland situated south of Åkrafjorden at the base of Prestafjellet at 59.44 ° N, 5.58 ° E. The landscape surrounding Tungesvikstranden is characterized by a changing topography with a steep slope from the sea level at Åkrafjorden to the top of the Prestafjellet mountain. Tungesvikstranda comprises a north-westerly exposed slope with a bedrock of granite and gabbro (Brekke 2001). Mean annual precipitation in the normal period 1961–1990 was 1949 mm; mean monthly precipitation was 176 mm in January and 123 mm in July (Førland 1993). The mean annual temperature 1961–1990 was 7.2˚C, with the coldest month being January (mean temperature 1.1˚ C) and the warmest month being July (mean temperature 14.2˚C ( Førland 1993, Aune 1993)). The weather stations on which these normals were based, were #47500, Etne (59.65 °N, 5.95 °E), #47600 Litledal (59.66°N, 6.07°E), #47820 Eikemo (59.86°N, 6.2786°E) and #47700 Åkrafjord (59.86°N, 6.02°E). The large amount of precipitation places this area in the strong oceanic vegetation section as defined by Moen et al. (1999). The woodland, a pasture-woodland, is situated in the boreonemoral vegetation zone (see Figure 2), and Tungesvikstranda is dominated by old pollards of *Fraxinus excelsior* mixed with various other deciduous trees, mainly *Alnus glutinosa*, *Alnus incana*, *Betula pubescens, Corylus avellana, Salix caprea* and *Sorbus aucuparia* (Tønsberg 1994).

**FIGURE 1 LOCATION OF TUNGESVIKSTRANDA**

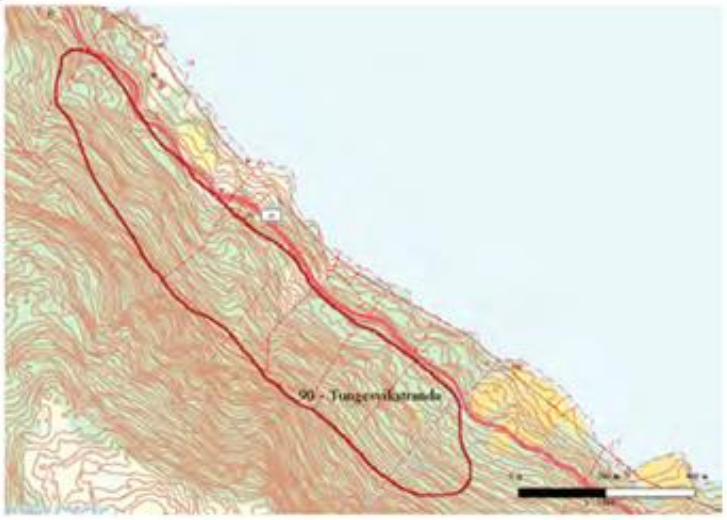



**FIGURE 2 MAP OF THE STUDY AREA (MODIFIED FROM GAARDER & FJELSTAD 2009)**

## SAMPLING DESIGN

In 2006, a part of the Tungesvikstranda locality was selected for a study on local distribution patterns of lichens (Myhre 2011). This area is traversed by country road 48 at about 40 m altitude from NW to SE. The study area of Myhre (2011) comprised a belt from the road upwards and westwards for a sufficient distance in order to encompass approximately 300 target trees, which were exactly georeferenced by the Total Station Theodolite Sokkia SET5F. Positions of all studied trees were recorded as coordinates in UTM zone 32, with a precision of 1 cm. This study uses a part of the study area of Myhre (2011), in which a subset of the trees studied by her was selected by a stratified random procedure (see below). The selected area contains deciduous forest, and was located in the south-eastern part of the area used by Myhre, which included the steepest altitudinal gradient. This was done in order to include as much of the variation due to elevation as possible. All ash trees in the area with a diameter above 20 cm, both pollarded and non-pollarded, were candidates for being included in the study.

Trees were selected at random from all realised combinations of the following three strata:

1) elevation above sea level
2) diameter larger or smaller than the average diameter in the respective height zone
3) pollarded or non-pollarded

The total altitudinal interval spanned by the study area was 178 m (59–237 meters above sea level), which was divided into four altitudinal zones (from low to high altitudes referred to as zones 1–4), each spanning 44.5 meters. Trees in each altitudinal zone were divided in two groups, a) trees with diameter larger than the average in the respective height zone and b) trees with smaller diameter than the average diameter in the respective height zone. This was done in order to represent variation in tree size (and age). In each diameter group in the respective height zone, six pollarded trees and six non-pollarded trees were randomly chosen. Ideally, this design ought to give 16 (4 × 2 × 2) groups with a total 96 trees. Some combinations of strata were, however, absent or represented by less than six trees among the 300 trees studied by Myhre (2011). This was the case for pollarded trees with diameter smaller than the average diameter in the respective zone, which were absent from altitudinal zone 1 and represented by only one tree in altitudinal zone 2. In zone altitudinal 4, no pollarded tree was found at all. The 13 groups that were represented in the study area had a total of 73 trees, which were randomly chosen from the total number of trees in each combination of strata.

## OBSERVATION UNITS

### ZONES

Each tree was divided into height zones and sectors to address variation within trees. The stem of each pollarded tree was divided into basis (zone 1), stem (zone 2), top (zone 3), pollarded crown (zone 4) and pollarded branches (zone 5) (see Figure 3). The limits between zones were set by criteria based on the change in tree-stem slope. The limit between basis and stem was set as the point where the maximum increase in slope angle took place. The limit between stem and top was set where the decrease in angle was largest, while the limit between top and pollarded branches was set at the base of the branches, *i.e*. where they diverge from the bowl. The pollarded crown was separated from the top by the change in slope into a more horizontal plane and thereby representing the upper side of the pollarded part of the bowl. The branches and the top were demarcated by the change in angle of the slope. The upper limit for the pollarded branches was set to ½ meter above their limit to the pollarded crown. The large variation in shape and size within and between the trees in different sizes between each observation unit (OU.) motivated for dividing into different zones between pollarded and non-pollarded trees.

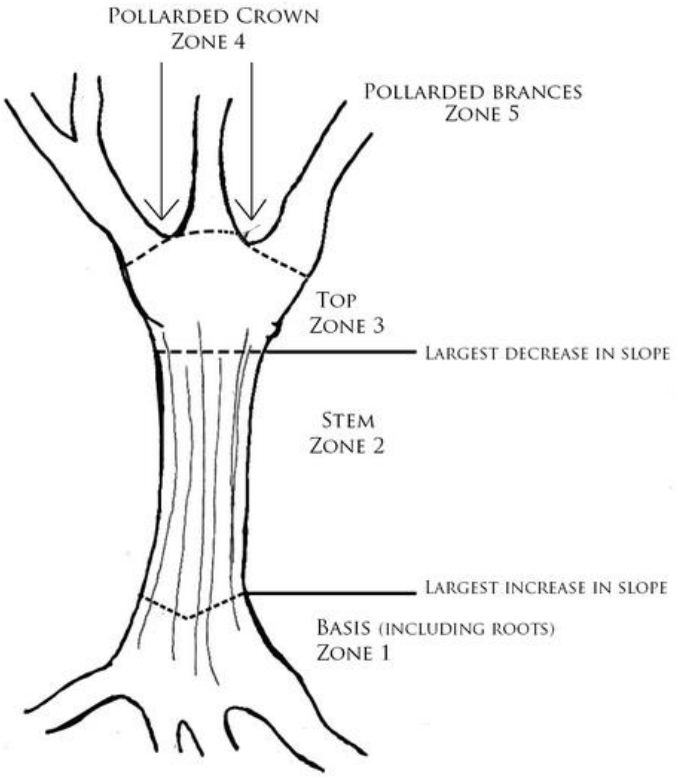



**FIGURE 3 ZONES OF POLLARDED TREE**

The stem of each non-pollarded tree was divided into basis (zone 1), lower stem (zone 2) and upper stem (zone 3) (see Figure 4). The limit between basis and lower stem was set as the point where the maximum increase in slope angle took place. The limit between the lower stem and upper stem was set at 2 meters from the highest point of the basis of the roots (vertical point of zero). The 2 m limit between the upper lower and upper stem zones corresponded to the mean upper limit of the stem zone of pollarded trees. Thus, the upper stem of non-pollarded trees corresponded to the top, pollarded crown and the pollarded branches zones of pollarded trees with respect to height above the ground. The upper limit of the upper stem zone was set to 3 meters above the vertical point of zero (the highest altitudinal point on the ground where there was exposed bedrock or soil).

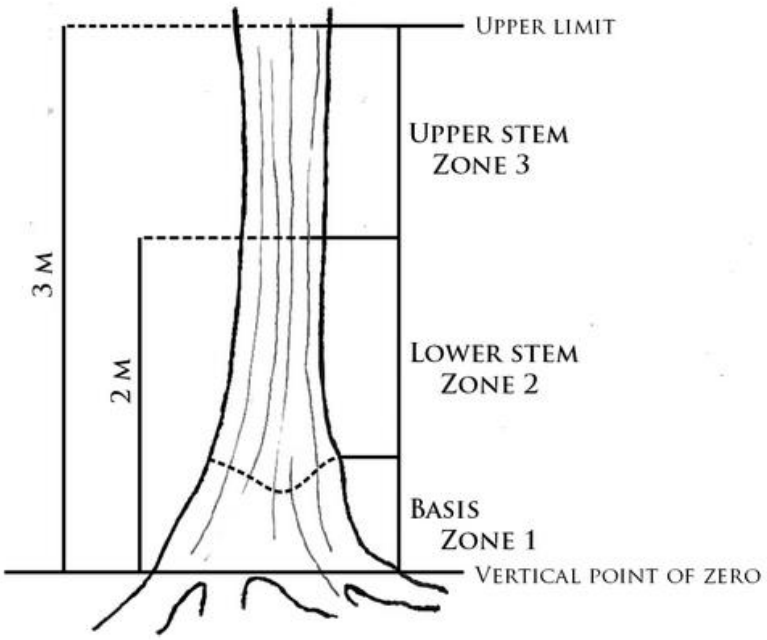
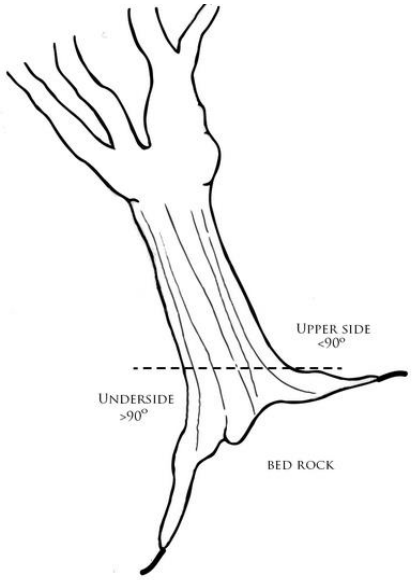



**FIGURE 4 ZONES OF NON-POLLARDED TREE**

SECTORS

The steepness of the ground made most tree stems in the area tilt downwards to a smaller or larger degree. This was the motivation for dividing each tree into four sectors (see figure 5 and 6), referred to as upper side (sector 1), right side (sector 2), underside (sector 3) and left side (sector 4), respectively. The upper side comprised the two sectors at each side of the compass direction at which the bole had its smallest slope (measured longitudinally along the bole, in direction of the tree top) and the underside, which were defined independent of the upper side, similarly comprised the two sectors at each side of the compass direction at which the bole had its largest slope (>90°). The right and the left side were defined as the sectors between the upper and undersides.

The 13 trees (#27, #35, #56, #77, #91, #92, #121, #122, #144, #157, #159, # 192 and #197) with vertical stems were divided into four 90° sectors.



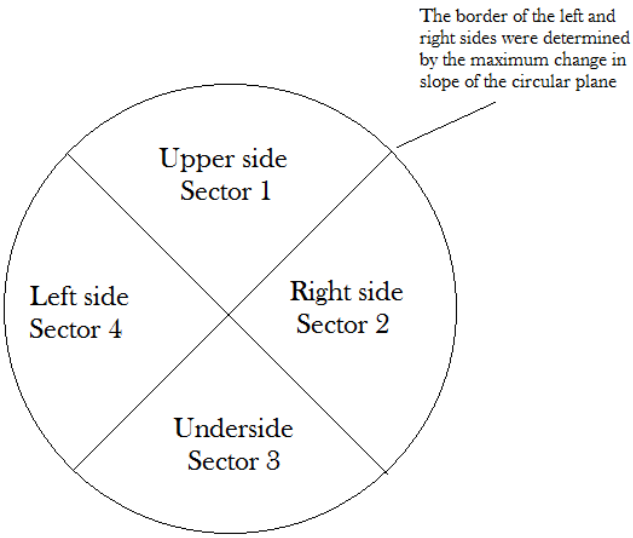




**FIGURE 5 ORIENTATION OF UPPER AND UNDERSIDE**

**FIGURE 6 CROSS SECTION OF THE TREE STEM**

The number of observation units (OUs), or zone-sectors, was 20 per pollarded tree (5 zones × 4 sectors) and 12 per non-pollarded tree (3 zones × 4 sectors). The total number of OUs was limited upwards to 1132 (32 pollarded trees x 20 zone-sectors = 640 OUs + 41 non-pollarded trees x 12 zone-sectors = 492 OUs), but not all of the trees comprised all potential zone-sectors, so the actual number of OUs was 1085.

### SAMPLING OF BRYOPHYTES

All species of bryophytes were recorded in each OU. Species quantities were recorded on an eight-step $\log_2$ percentage scale with values x = 1 corresponding to < 1% cover, x = 8 corresponding to > 64 % cover, and $x \in [2, 7] \Leftrightarrow 2^{x-2}$ % < cover < $2^{x-1}$ %. Some of the identification work was done *in situ*, but samples were collected whenever necessary for determination *ex situ*. In total 74 species were recorded. A list of species found is given in Appendix 1.

### RECORDING OF EXPLANATORY VARIABLES

Total bryophyte cover (Moss_cover), macrolichen cover (Lichen_cover) and exposed bark (Bark_cover) were measured in percent (%) in all observation units. Pollarding or non-pollarding was recorded as a binary variable; 0 = not pollarded, 1 = pollarded. Circumference at breast height (130 cm) was measured in centimetres. Canopy cover

(Canopy_cover) was measured for each sector perpendicularly to the tree circumference at the mid-point of the sector with a densiometer (Lemmon 1956). The fraction of moss cover at the line separating the tree base from the adjacent ground level (Moss_basis) was measured for each basis unit in percent (%), using a $\log_2$ scale that ranged from 1-8 (the same scale used for recording bryophyte species cover). For each sector, the aspect (in degrees) was measured (Northing). The mean grain (particle) size of the substratum (Mean_Grain) that surrounded the base of the tree was measured 0.5 meter from the base using Wentworth's scale (Wentworth 1922) which were transformed into a $\log_2$ scale (Φ-scale). The geographic coordinates recorded by Myhre (2011) were used in this study in analyses of spatial structure (see below). Measures were made by Theodolite Sokkia SET5F and recorded as positions (in UTM zone 32), broken down to three components: (1) x coordinate, (2) y coordinate and (3) z coordinate. The maximum (Slope_max) and minimum slope (Slope_min) of the tree stem in each observation unit, as well as the slope at the centre of the unit (Slope_C), measured longitudinally along the bole in direction of the tree top, was measured with a clinometer compass (divided in 400 degree units). As a measure for the trees inclination there was used the Slope_C value for the upper side of the stem OU. A sketch map of each tree drawn in the field by use of measurements of zone-sector borderlines was used to estimate the surface area of each zone-sector. Presence/absence of two types of microhabitats was also recorded: exposed, decaying wood and cavities. Affiliation with zone and sector, respectively, were recorded as ordinal variables: Zone of pollarded trees: 1 : basis; stem : 2; top : 3; pollarded crown : 4; and pollarded branches : 5. Zone of non-pollarded trees: 1 : basis; lower stem: 2; and upper stem: 3. Sector, regardless of pollarding or not: 1 : upper side; left side : 2; underside : 3; and right side: 4.

From the raw data matrix of abundance values for 1085 observation units, a derived data matrix of 567 consolidated observation units (COUs) was obtained by calculating the geometric mean abundance value for each species in (1) all four sectors in each zone, and (2) all five and three zones for each pollarded and non-pollareded tree in each sector, for the respective tree. The derived set thus comprised five and three zones for each pollarded and non-pollarded tree, respectively, and four sectors for each tree. Since all original observation units (zone-sector combinations) contributed to two COUs in the derived data set, the weight of each original OU in the subsequent analyses remained equal. The zones and sectors for the consolidated observation units will hereby be referred to as zonal COU's and sector COU's.

## DATA ANALYSES

Editing and manipulation of data were performed in Microsoft Office Excel(Anonymous 2009). All statistical analyses were done using R software version 2.15.2(team 2011). The vegan library (Oksanen 2012) version 2.0-6 was used for multivariate data analysis and the geoR library (Ribeiro and Diggle 2001)version 1.7-4 was used for geostatistics.

To reduce the skewness and decrease heteroscedastisity, all continuous variables were transformed to 'zero skewness' (Økland 2001) prior to analyses (Økland 1990b). This was done by finding the constant c that gives the transformed variables zero skewness. Depending on whether the distribution of each variable was skewed to the left or to the right, each variable was transformed by using the following formulae:

| | | |
|---|---|---|
| x left skewed: | $y=e^{cx}$ | skewness is negative (< 0) |
| x right skewed: | $y= \ln(c+x)$ | skewness is positive (> 0) |

In order to find the c-value that corresponded to minimum skewness, a manual iteration (in Excel) was performed. After transformation, all continuous variables were ranged onto a 0–1 scale by using the formula:

$$Z = \frac{y - y_{\min}}{y_{\max} - y_{\min}}$$

where $y_{min}$ is the minimum value for the environmental variable (y) and $y_{max}$ is the maximum value. Categorical (factor-type) variables were not transformed.

## RELATIONSHIP BETWEEN THE EXPLANATORY VARIABLES

To describe multivariate patterns in the distribution of explanatory variables Principal Component Analysis (PCA) (Pearson 1901) as used. Only continuous (and transformed) variables were included in the PCA ordination, due to PCA being an extension of the parametric linear regression and thereby assume a linear relationship between variables and the axes. To measure the strength of the pair-wise relationship between explanatory variables the Kendall's non-parametric correlation coefficient (Kendall 1938) was used. This was done for all explanatory variables, including binary variables.

### ORDINATION OF SPECIES COMPOSITION

For investigation of species composition, one heuristic and one geometric ordination method were applied in parallel in order to extract the gradient structure of the species-plot data matrix. Both methods order the observation units along axes of variation, that represent coenoclines (gradients in species composition;(Whittaker 1967)). The statistically based method used was Detrended Corresponding Analysis (DCA) (Hill 1979, Hill and Gauch 1980). DCA comes with two sets of eigenvalues, the 'DCA eigenvalue' and 'DECORANA values' (Oksanen 2012). Both were reported for comparability with other studies (Oksanen 2012). For the geometric methods both Local Non-metric Multidimensional Scaling (LNMDS) and Global Non-metric Multidimensional Scaling (GNMDS) were tested in a pilot study. Of these, LNMDS was preferred since its axes corresponded better with the axes of the DCA (*i.e.,* had higher pair-wise Kendall's correlation coefficients $\tau$ between corresponding axes). The specifications used for LNMDS were: distance measure = Bray-Curtis distance, dimensions = 2, initial configurations = 500, maximum iteration = 500, epsilon = 0.9 (cut-off value for regarding B-C distances as unreliable) and convergence ratio for stress = 0.9999999. LNMDS axes were linearly rescaled in half change units (H.C. units) to enhance comparability with the corresponding DCA axes. The two ordinations with lowest and closest matching stress value were found to be similar (P = 0.001; 999 permutations) in a Procrustes test(Oksanen 2012). The lowest-stress solution was used. Both ordinations were inspected for known artifacts like arch effect (in LNMDS), and edge or tongue effects (in DCA) or other potentially artifactual patterns (Økland 1990b, Økland and Eilertsen 1993).

DCA and LNMDS are considered complementary because of their essential differences. Therefore a similarity in the results of the two methods was taken as an indication that a reliable gradient had been found (Økland 1990b, Økland 1996). The non-parametric Kendall's correlation coefficient tau ($\tau$) was calculated for pair-wise DCA and LNMDS axes 1 and 2. Consistent configurations indicated that a realistic ordination had been achieved. The proposal of Liu et al. (2008) that ordination axes can be considered as similar when their pair-wise correlation coefficient $|\tau| > 0.4$ was used as a guideline.

### ECOLOGICAL INTERPRETATION OF ORDINATION AXES

The variation explained by each ordination axis at each of the two nested levels, between and within trees, was assessed using split-plot GLM analysis (*e.g.,*Auestad 2008). Split-plot GLM (*e.g.,* Crawley 2013) quantifies the total variation, the variation explained by each variable at each nesting level, and the residual variation at each nesting level. Tests of the null hypothesis that the variation explained by a variable at a specific nesting level was not higher than that of a random variable were evaluated. All explanatory variables were subjected to split-plot GLM analysis, with respect to both DCA ordination axes. I addition to the split-plot GLM analysis, the Kendall rank

correlation coefficient, tau (τ), was calculated for all continuous variables to reveal the direction the variable increased or decreased with each DCA axes (see Table 4). Only the sign of the coefficient were used (Auestad 2008).

To investigate variation of environmental variables in DCA ordination, all variables were fitted on to the DCA ordination diagram. Continuous explanatory variables were represented as arrows showing the strength of the correlation of the explanatory variables with the axes (Gabriel 1971), which also facilitated interpretation of the ordinations. The direction of arrows indicates the direction of maximum change in the variable while the length of the arrow indicates the relative rate of maximum change in this direction. Explanatory factor variables were also included as points, one for each factor level, which gives the mean COU score for the level along each axis. The enfit command in the vegan package was used to obtain DCA biplots.

DCA isoline diagrams were made for continuous and binary variables that explained significant amounts of variation ($\alpha = 0.05$) along at least one DCA axis at least one nesting level, using the ordisurf command in vegan.

### Analyses of spatial structure

Geostatistical methods, *i.e.,* semi-variograms (Rossi et al. 1992) were obtained to explore the spatial structure of continuous explanatory variables and DCA ordination axes (COU scores). Euclidian distance was used as measure of geographic distance. The slope of a semivariogram model fit to the empirical semi-variance values was used to evaluate the strength of spatial structure, together with envelopes obtained for each semi-variance value by the variog.mc.env command in the geoR package. A variable was considered to be spatially structured in the distance interval for which the observed semi-variance was increasing and outside the envelope. Because the zonal COU's and sector COU's within each tree had the same coordinates, a pilot semi-variogram was first made for the 73 trees to decide how to divide the range of distances into lag classes. A division into 12 lag classes, using 0.5-units on a 2-logarithmic scale were used: 1 : 0 – 8m; 2 : 8-11.3m; 3 : 11.3-16m; 4 : 16-22.6m; 5 : 22.6-32m; 6 : 32-45.3m, 7 : 45.3-64m, 8 : 64-90.5m; 9 : 90.5-128m; 10 : 128-181m; 11 : 181-256m; 12 : 256-309 m (the longest distance observed between two investigated trees). The class with the lowest number of tree pairs was lag class two with 210 tree pairs. To include variation between different zonal COU's and sector COU's within each tree in the analysis of spatial structure, two separate 'distance' matrices were made, one for zonal COU's and one for sector COU's, in each of which a number .1–.5 was added at to the coordinates of each tree to indicate affiliation to the different zonal COU's. For pollarded trees, the numbers .1-.5 were added to the x-coordinate as follows: .1 for basis; .2 for stem; .3 for top; .4 for pollarded crown; and .5 for pollarded branches. For non-pollarded trees the numbers .1-.3 were added to the x-coordinate as follows: 1 for basis; 2 for lower stem; and 3 for upper stem.'

For the sector COU's, a number was added to both x- and y-coordinates (see figure 7). To represent the upper side, .1 was added to the x-coordinate and .2 to the y-coordinate. The left side was represented by adding .1 to the x-coordinate and .1 to the y-coordinate, the underside by adding .2 to the x-coordinate and .1 to the y-coordinate, and the right side was represented by adding .2 to the x-coordinate and .2 to the y-coordinate, as shown in figure 7.

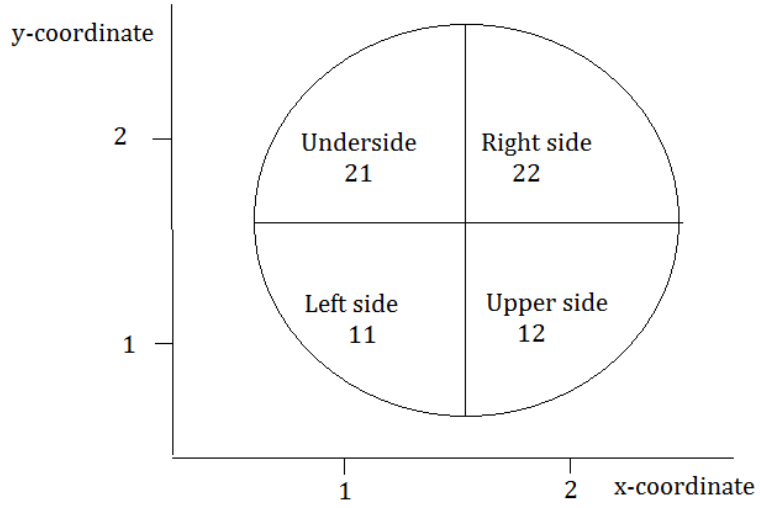



**FIGURE 7 ADDING OF NUMBERS TO X- AND Y-COORDINATES TO SECTORS, THE CIRCLE REPRESENT A CROSS SECTION OF THE TREE STEM.**

### CONSTRAINED ORDINATION

To investigate the strength of the relationship between the binary factor variable, pollarding, and the distribution of moss species on the investigated trees, a constrained ordination by canonical correspondence analysis (CCA), was carried out. It was also investigated if there was a significant amount of variation that could be explained by pollarding after the effect of Circumference had been accounted for. The data matrix used for this analysis were the zonal COU's since the CCA cannot be applied to data with missing values (NA) and therefore could not handle the entire COU data matrix. The fraction of variation explained (FVE) was calculated by use of inertia values given by the CCA. However, FVE needs to be interpreted with caution because the total inertia includes variation explained by polynomial distortion axis and therefore underestimates the true variation explained by the environmental variable (Økland 1999). A Monte Carlo permutation test (in vegan, with 100 permutations) was performed in order to test the null hypothesis that the relationship between pollarding and species distribution was not stronger than expected of a random binary variable.

# RESULTS

## DATA PROPERTIES

The study area contained 73 trees of which 32 were pollarded and 41 were not pollarded. Of the pollarded trees, 30 trees included all five zones while two trees (#52 and #91) only included three zones [the top (zone 3) and the pollarded crown zones (zone 4) were missing due to the absence of change in slope between the zones which made the criterion for zonal division impossible to apply]. In total, the 279 zone COUs were distributed on 156 zone COUs for pollarded trees (each tree with up to five zone COUs) and 123 zonal COUs for non-pollarded trees (each with three COUs). Of the 73 trees, 69 (all except trees #27, 35, 154 and 161) contained a total of 288 sector COUs; the reason for missing sector COUs was presence of microhabitats, which were investigated separately. There were 70 of the sector COUs that contained microhabitat with decaying wood, of which 41 were on pollarded trees and 63 of the COU's contained microhabitat with cavities, of which 47 were situated on pollarded trees.

The range of Moss_cover in COU's varied between 6 and 100 %, with a mean of 44 % coverage. The range of Lichen_cover varied between 0 and 64 %, with a mean of 10 %. Bark_cover had a range of variation between 0 and 93 % cover and a mean of 47 %. The range in Circumference was 65 – 418 cm, with a mean at 217.7 cm. Slope_C of the COU's had a range of 0-96.5° and a mean of 20.9°. Slope_min varied between 0–62°, with a mean of 9.5°, while Slope_max had a range of 13.3 – 100°, with a mean of 32.4°. Slope_tree ranged between 100° and 137° (circle divided into 400 degree-units) with a mean of 110.7°, implying that the trees varied from being vertical to making an angle of 37° with the vertical plane. The range of variation in other recorded variables is given in Table 1.

The number of species in each of the 1085 OU's was generally low and more than half of all OU's included less than five species (see Figure 8).

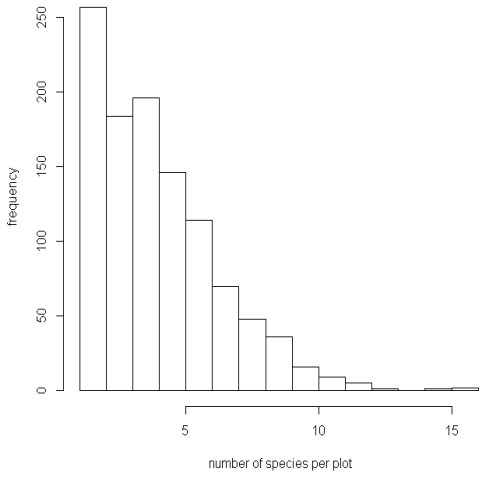



**FIGURE 8 FREQUENCY DISTRIBUTION FOR NUMBER OF SPECIES PER OU IN THE FULL SET OF 1085 OUS**

**TABLE 1 SUMMARY OF EXPLANATORY VARIABLES**

| Abbreviations | Variable | Unit of measurement | Summary statistics of untransformed variable | | Transformation | | Variable type C = continuous F = *factor* |
|---|---|---|---|---|---|---|---|
| | | | Range | Mean | Type | C-value | |
| **Epiphyte cover properties** | | | | | | | |
| Moss_cover | Bryophyte cover | % | 6.13-100 | 42.8 | ln(c+x) | 42.839 | C |
| Bark_cover | Bark cover | % | 0-93 | 47 | e^cx | 0.0054635 | C |
| Lichen_cover | Macrolichen cover | % | 0-64.3 | 9.7 | ln(c+x) | 2.9988 | C |
| **Geographic position variables** | | | | | | | |
| Easting | X co-ordinate | - | (-6568)-(-6113) | (-6304) | e^cx | 0.003 | C |
| Northing | Y co-ordinate | - | 6656543-6656878 | 6656721 | e^cx | 0.001 | C |
| **Tree properties** | | | | | | | |
| Pollarding | Pollarding of the tree | presence/absence (1/0) | - | - - | | - | F |
| Circumference | Circumference at Brest height | cm | 65-418 | 217.1 | ln(c+x) | 223.18 | C |
| Slope_tree | Slope at the upper side of the stem sector. Measured at the center of the OS | -200°-200° | 100-137 | 110.7 | e^cx | 51.089 | C |
| **Sector properties** | | | | | | | |
| Canopy_cover | Absence of canopy cover | % | 2-19.1 | 7.3 | ln(c+x) | 3.786 | C |
| Grain_mean | Grain size surrounding base of tree | Wentworth's grain size scale in cm ($log_2$) | -2 – 10 | 2.8 | ln(c+x) | 11.386 | C |
| Northing | Slope | O -360° | 0-360 | 164.5 | ln(c+x) | 1161.6 | C |
| Moss_basis | Continuous bryophyte cove at basis and onto ground | 1-8 (2log scale (%)) | 0-8 | 5.3 | e^cx | 0.12384 | C |
| **Zone-sector properties** | | | | | | | |
| Slope_C | Slope at centre of observation unit | -100°- 100° | -27.6-96.5 | 20.9 | ln(c+x) | 52.979 | C |
| Slope_min | Minimum slope at observation unit | -100°- 100° | -62-27.6 | 6.9 | ln(c+x) | 55.7188 | C |
| Slope_max | Maximum slope at observation unit | -100°- 200° | -15-100 | 25.1 | ln(c+x | -90.187 | C |
| Decaying_wood | Microhabitat consisting of decaying wood | presence/absence (1/0) | - | | - | - | F |
| Cavity | Microhabitat consisting of cavity | presence/absence (1/0) | - | | - | - | F |

## RELATIONSHIP BETWEEN EXPLANATORY VARIABLES

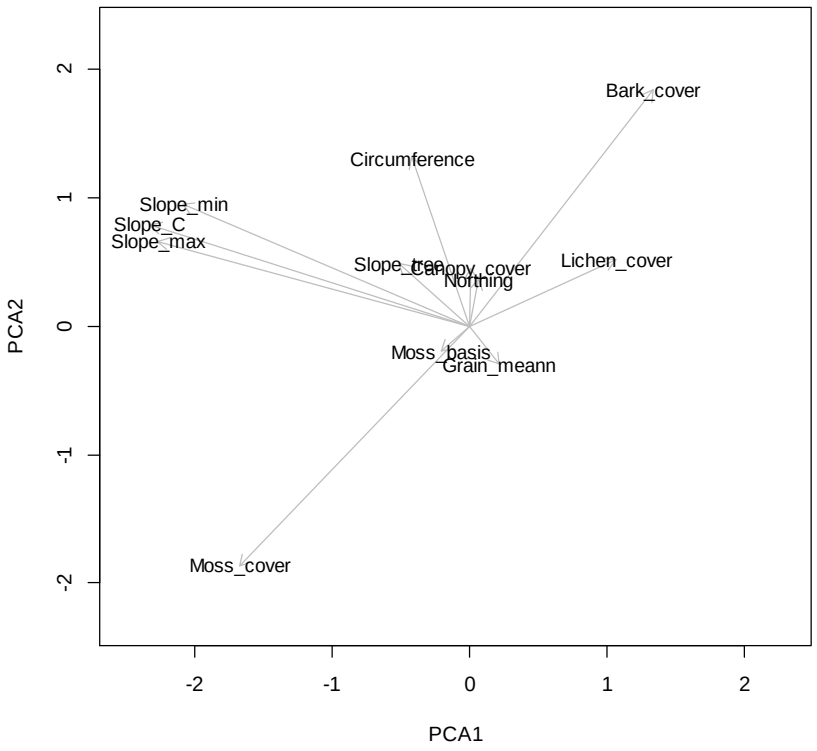
### PCA

The first PCA axis explained 25.76% of the total variation in the matrix of 11 continuous explanatory variables. The eigenvalue for the PCA axes 1-4 were 3.09, 1.69, 1.20 and 1.18, corresponding to 25.76%, 14.04%, 9.98% and 9.82% of the total variation in the dataset, respectively (see Table 2).

**TABLE 2 PCA AXES 1-4: EIGENVALUES AND VARIATION EXPLAINED**

| | ***PCA 1*** | ***PCA 2*** | ***PCA 3*** | ***PCA 4*** |
|---|---|---|---|---|
| *Eigenvalues* | 3.0895 | 1.6852 | 1.19719 | 1.1785 |
| *Proportion Explained* | 0.2575 | 0.1404 | 0.09977 | 0.0982 |
| *Cumulative Proportion* | 0.2575 | 0.3979 | 0.49766 | 0.5959 |

The continuous explanatory variables that had the strongest relationship with PCA axis 1 were circumference; slope variables (Slope_C, Slope_max and Slope_min); and cover variables (moss, lichen and bark cover). Their strong relationship with the axis was indicated by the long vectors in Fig. 9. Slope_C, Slope_min, Slope_max, circumference and Moss_cover were negatively correlated with PCA axis 1, while Bark_cover and Lichen_cover were positively correlated with this axis. Northing, Canopy_cover, Grain_mean and Moss_basis all had short vectors which indicated a weak relationship with the first PCA axis. The second PCA axis explained variation in all continuous explanatory variables, with the exception of Moss_basis. The variables that had the strongest relationship with this axis were circumference, Bark_cover, Lichen_cover and Moss_cover, of which all had long vectors with a significant component also along axis 1. This indicated that these variables had a strong relationship with both axes. Circumference, Slope_tree and Lichen_cover had a strong negative relationship with the third axis. Canopy_cover, Moss_basis, Bark_cover and Grain_mean were positively correlated with the axis. PCA axis 4 was not considered because little additional variation was explained by this axis.



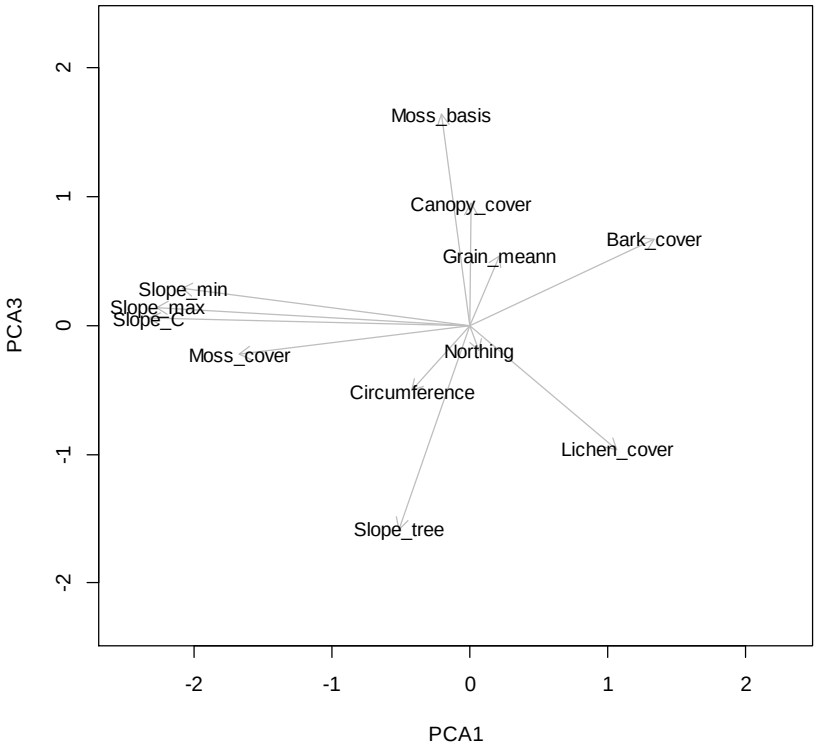




**FIGURE 9 PCA ORDINATIONS OF CONTINUOUS VARIABLES: AXES 1 AND 2 TO THE LEFT AND AXIS 1 AND 3 TO THE RIGHT. THE LENGTH OF THE VARIABLE VECTORS INDICATES THE STRENGTH OF THE RELATIONSHJIP BETWEEN THE VARIABLE AND THE ORDINATION AXES.**

## CORRELATION ANALYSIS

Values of the Kendall rank correlation coefficient, tau (τ) calculated between the continuous explanatory variables and the PCA axis (see Appendix 2) confirmed that Moss_cover was negatively related with Lichen_cover and Bark_cover positively related with the slope variables. It also showed that Moss_cover and circumference was not significant.

## ORDINATION OF SPECIES COMPOSITION

DCA ordinations were first made for the set of 1085 OUs, but the result was strongly affected by outliers as a consequence of the large number of OU's that contained few species (Fig. 1). Instead, the 567 COUs were subjected to ordination. DCA axes 1 to 4 based upon 567 COUs had eigenvalues of 0.2865, 0.2751, 0.2089 and 0.2130, respectively (see Table 3).

**TABLE 3 PROPERTIES OF DCA AXIS 1-:4: EIGENVALUES AND GRADIENT LENGTHS IN S.D. UNITS.**

| | ***DCA 1*** | ***DCA 2*** | ***DCA 3*** | ***DCA 4*** |
|---|---|---|---|---|
| *Eigenvalues* | 0.2865 | 0.2751 | 0.2089 | 0.2130 |
| *Decorana values* | 0.3254 | 0.2571 | 0.2070 | 0.1865 |
| *Axis lengths (S.D. units)* | 3.4431 | 3.3628 | 2.9532 | 2.8070 |

Gradient lengths of DCA axes 1 and 2 were 3.44 and 3.37 S.D. units, respectively. The COU's were evenly distributed along the first two DCA axes (see Figure 10), except for a small tendency for lower density towards the fringes. No obvious distortions (polynomial distortions, tongue- or trumpet-shaped point configurations, presence of outliers or other deviant visual patterns) could be seen.

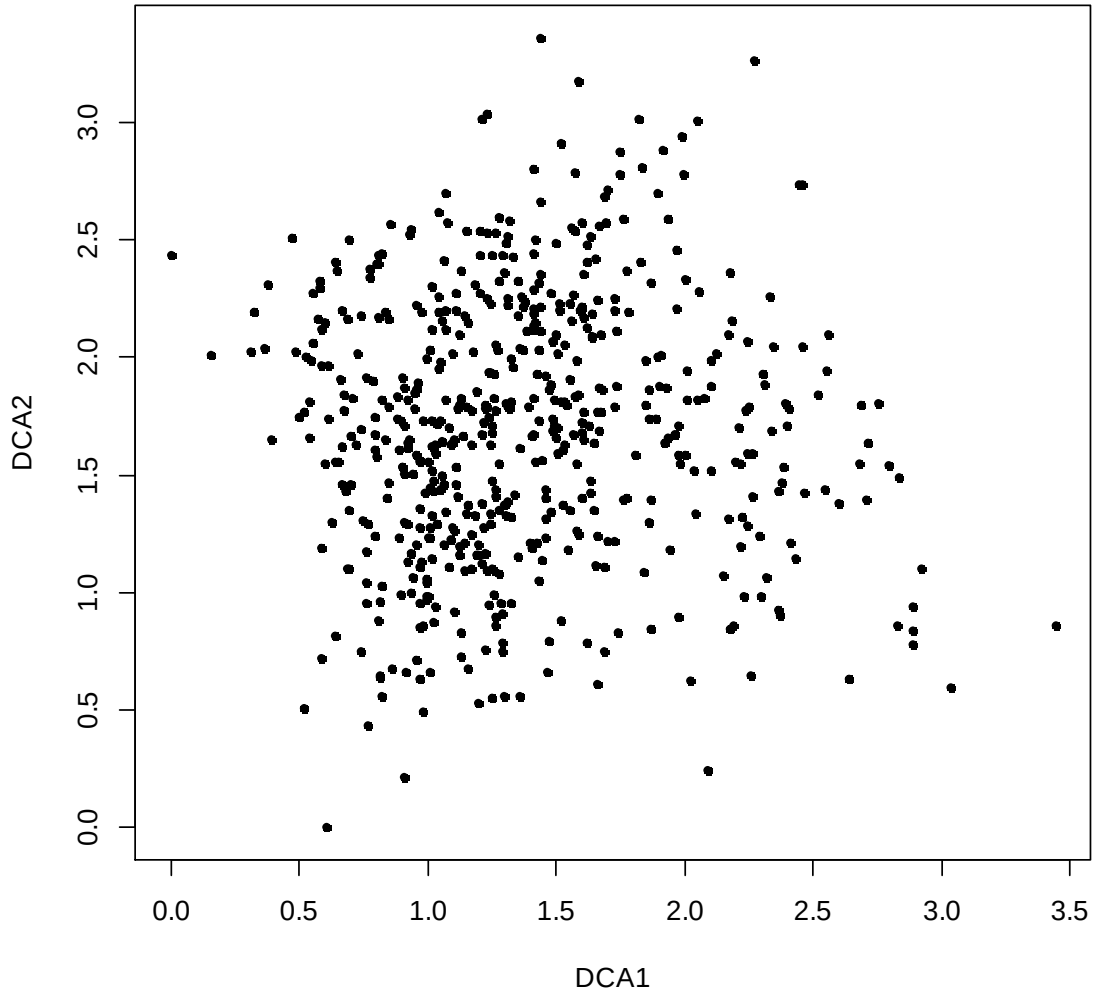



**FIGURE 10 DCA ORDINATION OF THE SPECIES COMPOSITION OF 567 COUS. AXES SCALED IN S.D. UNITS.**

Gradient lengths of the two dimensional LNMDS axes 1 and 2 were 1.970 and 0.913 H.C. units, respectively (see Figure 11). The scores for COU's were evenly distributed along the two first axes, although there was a slight decrease in density at the lower end of axis 2. There were no trends of polynomial distortion of the axes (tongue, trumpet or arch effects), nor any presence of outliers or other visual patterns.

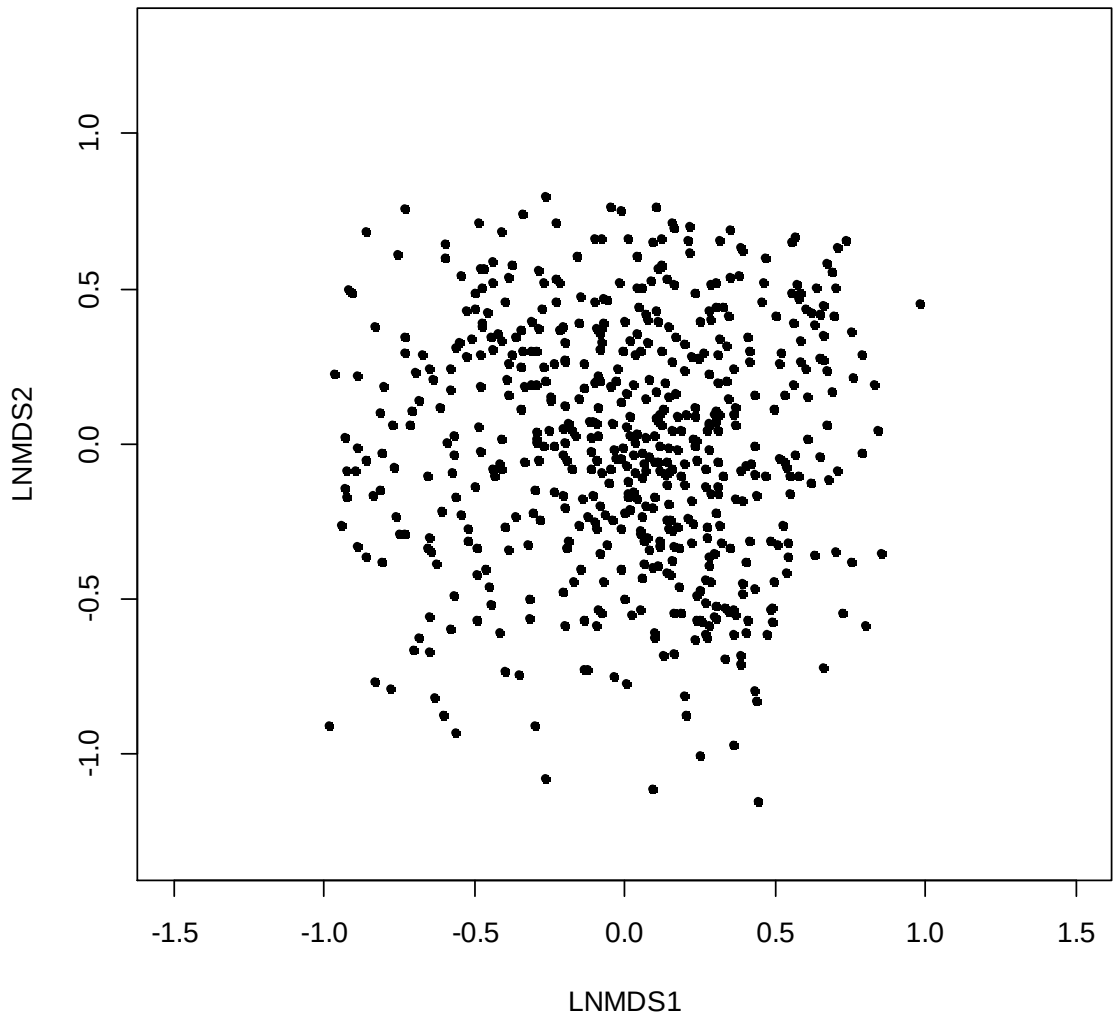



**FIGURE 11 LNMDS ORDINATION OF THE SPECIES COMPOSITION OF 567 COUS. AXES SCALED IN H.C. UNITS.**

### COMPARISON OF ORDINATIONS

Kendall's correlation coefficient, τ, calculated between pairs of ordination axes, showed that the first and second axes of DCA and LNMDS ordinations were strongly correlated: τ=0.626 between DCA axis 1 and LNMDS axis 1, and τ=0.604 between DCA axis 2 and LNMDS axis 2. The absence of polynomial distortions in both DCA and LNMDS was taken as a strong indication that the true structure in the species plot data matrix had been found. A search for a third strong gradient in the data, by correlating DCA axis 3 and the third axis of three-dimensional LNMDS, failed to prove existence of such a gradient (τ= 0.052, P = 0.06179). The fact that the two ordination methods revealed similar COU configurations in two dimensions, both without obvious artifacts, was taken as a strong indication that the main gradient structure had been found. Since the DCA ordination

gives estimates for species optima related to the ordination axes, this ordination was chosen for further analysis.

## ECOLOGICAL INTERPRETATION OF ORDINATION AXES

### GENERALIZED LINEAR MODEL – SPLIT PLOT ANALYSIS

#### RELATIONSHIP BETWEEN DCA AXIS 1 AND EXPLANATORY VARIABLES

Of the total variation in COU scores along DCA axis 1, 61.7 % was variation between trees ($SS_{TB}$) and 38.4 % was variation between COUs within trees (Table 4). The variables that explained significant fractions of variation along DCA axis 1 at the between-trees level ($SS_{EB}$/ $SS_{TB}$) were Moss_cover (0.09) and Circumference (0.09). The Kendall rank correlation coefficient, tau (τ), calculated between ordination exes and explanatory variables, showed that the relationship between the continuous explanatory variables and DCA axis 1 were positive for Moss_cover and negative for circumference (see Kendall's tau, Table 4). The variables that explained the largest fraction of variation in terms of total variation explained within trees ($SS_{EW}$/ $SS_{TW}$) for DCA axis 1 were Sectors (0.03) and Lichen_cover (0.02). Moss_cover (0.06) and circumference (0.05) were the variables that explained the largest fraction of the total variation, within and between trees ($SS_{TBW}$) taken together, for DCA axis 1.

#### RELATIONSHIP BETWEEN DCA AXIS 2 AND EXPLANATORY VARIABLES

Of the total variation in COU scores along DCA axis 2, 39.8 % was variation between trees ($SS_{TB}$) and 60.2 % was variation between COUs within trees (Table 4). The variables that explained significant fractions of variation along DCA axis 1 at the between-trees level ($SS_{EB}$/ $SS_{TW}$) were Moss_cover (0.33), Zones (0.33), Bark_cover (0.24), Lichen_cover (0.18) and Slope_max (0.14). Kendall's τ revealed a positive relationship between the continuous explanatory variables and DCA axis 1 for Moss_cover and Slope_C, and a negative relationship for Bark_cover and Lichen_cover (see Kendall's tau, Table 4). Zones (0.22) and Moss_cover (0.21) were the variables that had the largest fraction of the total variation explained ($SS_{TBW}$) for DCA axis 2.

**TABLE 4 GLM SPLITPLOT ANALYSIS OF COU SCORES FOR DCA AXIS 1 IN ORDINATION OF 567 COUS. THE STRENGTH OF THE RELATIONSHIP BETWEEN EACH EXPLANATORY VARIABLE (SEE TABLE X FOR OVERVIEW OF VARIABLES AND EXPLANATION OF ABBREVIATED VARIABLE NAMES) AND THE AXIS WAS EVALUATED SEPARATELY FOR THE BETWEEN-TREE AND WITHIN-TREE NESTING LEVELS. SIGN OF KENDALL'S TAU SHOW THE SIGN OF THE RELATIONSHIP (+/-) BETWEEN DCA AXIS 1 AND ENVIRONMENTAL VARIABLES.**

| DCA- axis 1 | Variation between trees<br>df: 71 $SS_{TB}$: 103.22 (= 61.66 %) | | | | | Variation within trees<br>$SS_{TW}$: 64.18 (= 38.34 %) | | | | | | Sign of Kendall's tau | Total variation<br>$SS_{TBW}$:167.4 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Variables: | **$SS_{EB}$** | **$SS_{RB}$** | **$SS_{EB}$/ $SS_{TB}$** | **F** | **p** | **df** | **$SS_{EW}$** | **$SS_{RW}$** | **$SS_{EW}$/ $SS_{TW}$** | **F** | **p** | **+/- (τ)** | **$SS_{EB+}SS_{EW}$ / $SS_{TBW}$** |
| Circumference | 9.24 | 93.98 | 0.090 | 6.984 | **0.010** | – | 0 | 64.18 | 0 | 0 | 0 | - | 0.052 |
| Slope_C | 1.58 | 101.64 | 0.015 | 1.105 | 0.297 | 493 | 1.18 | 63.00 | 0.018 | 9.255 | **0.002** | + | 0.016 |
| Slope_min | 2.25 | 100.98 | 0.022 | 1.581 | 0.213 | 493 | 0.73 | 63.45 | 0.011 | 5.654 | **0.018** | - | 0.018 |
| Slope_max | 0.31 | 102.91 | 0.003 | 0.216 | 0.643 | 493 | 1.17 | 63.01 | 0.018 | 9.123 | **0.003** | + | 0.001 |
| Slope_tree | 3.25 | 99.98 | 0.033 | 2.305 | 0.133 | – | 0 | 64.18 | 0 | 0 | 0 | - | 0.019 |
| Moss_cover | 9.33 | 93.89 | 0.090 | 7.057 | **0.010** | 493 | 0.76 | 63.42 | 0.011 | 5.883 | **0.016** | + | 0.060 |
| Lichen_cover | 0.94 | 102.29 | 0.001 | 0.653 | 0.422 | 493 | 1.39 | 62.79 | 0.021 | 10.930 | **0.001** | - | 0.014 |
| Bark_cover | 1.51 | 101.72 | 0.015 | 1.052 | 0.309 | 493 | 0.07 | 64.11 | 0 | 0.521 | 0.471 | - | 0.001 |
| Canopy_cover | 2.77 | 100.46 | 0.027 | 1.958 | 0.166 | 493 | 0.00 | 64.18 | 0.002 | 0.762 | 0.983 | - | 0.017 |
| Moss_basis | 2.69 | 100.54 | 0.026 | 1.899 | 0.173 | 493 | 0.16 | 64.02 | 0 | 1.225 | 0.269 | + | 0.017 |
| Grain_mean | 0.63 | 102.59 | 0.006 | 0.438 | 0.510 | 493 | 0.27 | 63.91 | 0 | 2.069 | 0.151 | + | 0.001 |
| Northing | 2.06 | 101.16 | 0.020 | 1.447 | 0.233 | 493 | 0.46 | 63.71 | 0.001 | 3.595 | 0.059 | - | 0.015 |
| Zone | 1.22 | 50.92 | 0.055 | 1.707 | 0.196 | 205 | 0.33 | 38.03 | 0.001 | 1.764 | 0.186 | | 0.001 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sector | 2.18 | 51.26 | 0.041 | 3.022 | 0.087 | 214 | 0.67 | 22.77 | 0.029 | 6.556 | **0.011** | | 0.017 |
| Pollarding | 2.6 | 100.6 | 0.025 | 1.835 | 0.18 | – | 0 | 64.18 | 0 | 0 | 0 | | 0.016 |
| Cavity | 2.54 | 100.69 | 0.025 | 1.788 | 0.185 | 493 | 0 | 64.18 | 0 | 0 | 0.995 | | 0.015 |
| Decaying_wood | 4.65 | 98.57 | 0.045 | 3.351 | 0.071 | 439 | 0.27 | 63.90 | 0.004 | 2.115 | 0.146 | | 0.029 |

**TABLE 5 GLM SPLITPLOT ANALYSIS OF COU SCORES FOR DCA AXIS 2 IN ORDINATION OF 567 COUS. THE STRENGTH OF THE RELATIONSHIP BETWEEN EACH EXPLANATORY VARIABLE (SEE TABLE X FOR OVERVIEW OF VARIABLES AND EXPLANATION OF ABBREVIATED VARIABLE NAMES) AND THE AXIS WAS EVALUATED SEPARATELY FOR THE BETWEEN-TREE AND WITHIN-TREE NESTING LEVELS. SIGN OF KENDALL'S TAU SHOW THE SIGN OF THE RELATIONSHIP (+/-) BETWEEN DCA AXIS 1 AND ENVIRONMENTAL VARIABLES.**

| DCA-axis 2 | Variation between trees<br>df: 71 $SS_T$: 72.55 (39.79%) | | | | | Variation within trees<br>$SS_T$: 109.8 (60.21%) | | | | | | Sign of Kendall's tau | Total variation<br>$SS_{TBW}$:182.35 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Variables: | $SS_{EB}$ | $SS_{RB}$ | $SS_{EB}$/ $SS_{TB}$ | F | p | df | $SS_{EW}$ | $SS_{RW}$ | $SS_{EW}$/ $SS_{TW}$ | F | p | **+/- (τ)** | $SS_{EB+}SS_{EW}$ / $SS_{TBW}$ |
| Circumference | 7.42 | 65.13 | 0.102 | 8.087 | **0.006** | 494 | 0 | 109.80 | 0 | 0 | 0 | - | 0.040 |
| Slope_C | 5.43 | 67.12 | 0.075 | 5.746 | **0.019** | 493 | 12.26 | 97.53 | 0.112 | 61.98 | **<0.001** | + | 0.097 |
| Slope_min | 1.55 | 71.00 | 0.021 | 1.551 | 0.217 | 493 | 9.95 | 99.84 | 0.090 | 49.15 | **<0.001** | + | 0.063 |
| Slope_max | 4.47 | 68.08 | 0.061 | 4.665 | **0.034** | 493 | 15.79 | 93.99 | 0.144 | 82.84 | **<0.001** | + | 0.111 |
| Slope_tree | 0.01 | 72.54 | 0.033 | 0.008 | 0.929 | – | 0 | 64.18 | 0 | 0 | 0 | + | <0.001 |
| Moss_cover | 2.39 | 70.16 | 0.033 | 2.42 | 0.124 | 493 | 36.18 | 73.61 | 0.330 | 242.30 | **<0.001** | + | 0.212 |
| Lichen_cover | 0.79 | 71.76 | 0.011 | 0.783 | 0.379 | 493 | 19.51 | 90.28 | 0.178 | 106.50 | **<0.001** | - | 0.111 |
| Bark_cover | 1.87 | 70.67 | 0.026 | 1.883 | 0.174 | 493 | 26.40 | 83.39 | 0.240 | 156.10 | **<0.001** | - | 0.150 |
| Canopy_cover | 4.24 | 68.31 | 0.058 | 4.407 | **0.039** | 493 | 0.02 | 109.77 | >0.001 | 0.01 | 0.905 | + | 0.023 |
| Moss_basis | 4.31 | 68.24 | 0.059 | 4.486 | **0.038** | 493 | 0.27 | 109.52 | 0.002 | 1.21 | 0.271 | + | 0.025 |
| Grain_mean | 0.44 | 72.10 | 0.006 | 0.436 | 0.511 | 493 | 0 | 109.80 | >0.001 | 0 | 0.995 | + | 0.002 |
| Northing | 0.02 | 72.53 | >0.001 | 0.017 | 0.897 | 493 | 0.10 | 109.70 | >0.001 | 0.48 | 0.495 | - | <0.001 |
| Zone | 4.65 | 33.16 | 0.064 | 9.967 | 0.002 | 205 | 35.69 | 44.42 | 0.325 | 164.70 | **<0.001** | | 0.221 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sector | 0.19 | 35.99 | 0.005 | 0.366 | 0.547 | 214 | 0.848 | 26.415 | 0.032 | 6.87 | **0.010** | | 0.006 |
| Pollarding | 4.94 | 67.61 | 0.068 | 5.182 | **0.026** | 494 | 0 | 109.8 | 0 | 0 | 0 | | 0.027 |
| Cavity | 1.69 | 70.86 | 0.023 | 1.694 | 0.197 | 493 | 1.22 | 108.57 | 0.011 | 1.69 | 0.197 | | 0.016 |
| Decaying_wood | 0.31 | 72.24 | 0.004 | 0.303 | 0.584 | 493 | 3.79 | 106.00 | 0.034 | 17.61 | **<0.001** | | 0.022 |

## VARIATION OF ENVIRONMENTAL VARIABLES IN DCA ORDINATION DIAGRAMS

Fitting environmental variables to the two-dimensional DCA ordination diagram (Fig. 12) to a large extent confirmed the relationships between variables and axes revealed by split-plot GLM analyses. The two variables most strongly related to DCA-axis 1 at the between-tree level, Circumference and Moss_cover, also obtained the longest vectors in Fig. 12, indicating that these variables best explained variation in species composition at that scale. Fig. 12 also shows that vectors for many other variables that were significantly related to DCA axes 1 or 2 in the split-plot GLM analysis, on one or both nesting levels, pointed in the same direction as Circumference or Moss_cover. This applied to Lichen_cover, Bark_cover (negatively related to Moss_cover) and Moss_basis and Slope_max (positively related to Moss_cover). The isoline diagram confirmed this trend: the contour lines for Moss_cover showed a steady decrease towards the upper part of the second axis (see Figure 14, Moss_cover) while lines for Lichen_cover showed the opposite trend (see Figure 15, Lichen_cover). This illustrated that high moss cover on trees was accompanied with lower lichen cover, in accordance with Figure 12.

All slope variables increased along the second axis, but also showed a small decrease along the first axis (see Figure, Slope_C, Slope_min and Slope_max). This confirms the result for the GLM split-plot where these variables were significantly related to both axes, but had a stronger correlation with the second axis than with the first. The GLM split plot also showed that the slope variables were more strongly significantly explaining variation within trees than between trees. Figure 14 and 15 for the slope variables illustrated this relationship with the contour lines following the transition between zones; increasing along the second axis with decreasing height of the tree. Canopy cover and vectors for some slope variables pointed more or less in a direction at right angles to that of Circumference and cover values, indicating a tendency for these variables to explain variation that was independent of the variation explained by the main group of variables (see Figure 5). In the GLM split-plot analysis, Moss_basis and Canopy_cover only explained significant amounts of variation along DCA axis 2, and, accordingly, accounted mainly for variation between trees. The isoline diagram accords with this (see Figure 15 Canopy_cover).

Zone centroids made up a series that aligned along the upper right-to-lower left direction in the ordination diagram (Fig. 12), with zone 1 near the high moss-cover end of a gradient and zone 3 near the low moss-cover end. These patterns were independent of pollarding, indicating that the species composition of basis and stem zones were similar between non-pollarded and pollarded trees. Zone 4 of pollarded trees occupied a position close to that of zone 2, indicating similarity in species composition with the stem zone. Zone 5 of pollarded trees occupied an isolated position near the low-canopy-cover corner of the ordination diagram (Fig. 12). This indicated that the branches of pollarded trees had a species composition that differed from all other zones, typical of trees with open crowns.

Also the sector centroids aligned along the line in the ordination diagram from upper right to lower left, but were placed closer to the origin than zone centroids. This showed that zones differed less in species composition than did zones. Only sector 3 (the underside) had a species composition that was distinctly different from the others, more similar to zones higher up on the tree.

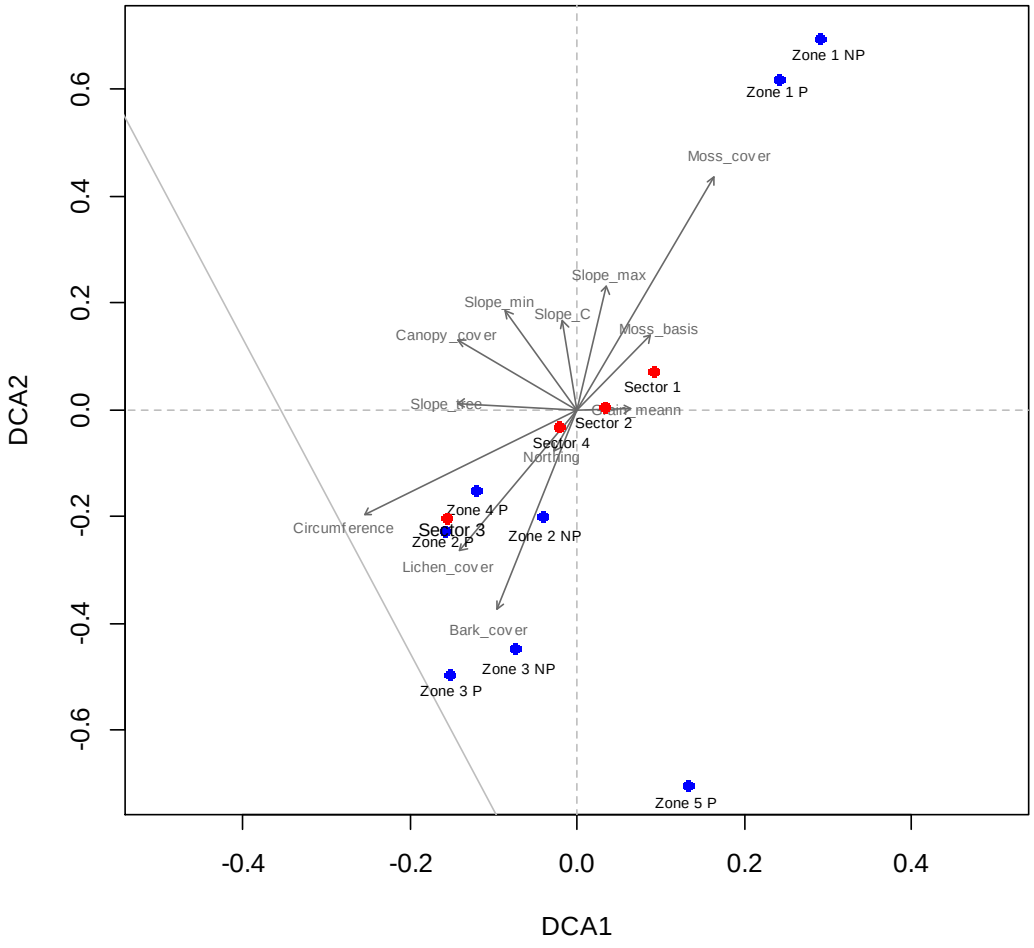



**FIGURE 12 SELECTED ENVIRONMENTAL VARIABLES FITTED TO THE DCA ORDINATION, AXES 1 AND 2. AXES ARE SCALED IN S.D. UNITS. CONTINUOUS VARTIABLES ARE REPRESENTED BY VECTORS POINTING IN THE DIRECTION OF MAXIMUM INCREASE OF THE VARIABLE, CATEGORICAL VARIABLES ARE REPRESENTED BY THE CENTROID OF EACH FACTOR LEVEL. P DESKRIBES POLLARDED AND NP DESKRIBES NON-POLLARDED TREES**

The centroids for presence of specific microhabitats, Decaying_wood 1 and Cavity 1, all occupied positions that could be projected onto the positive circumference vector and the negative Moss_cover vector (see Fig. 13). This indicated that these microhabitats were more frequent on large trees and trees with high moss cover than *vice versa*. The centroid for presence of Decaying_wood also occupied that could be projected onto the

positive Canopy_cover and Slope_tree vector, indicating an increase decaying wood on trunks with reduced canopy over and increased inclination of the tree. The centroid for presence of cavities (Cavity 1) was more frequent on pollarded trees than non-pollarded trees, while Decaying_wood 1 was independent of pollarding. The centroids for absence of microhabitat, Decaying_wood 0 and Cavity 0, occupied positions that could be projected onto the positive Bark_cover and Lichen_cover vector, indicating that trees with increased cover of bark and lichen had a lower frequency of these microhabitats.

The centroids for pollarded trees (pollarding 1) in Fig. 13 where at the lower end of both DCA axis 1 and 2, indicating an increasing in Bark_cover, Lichen_cover and circumference and a decrease in Moss_cover, while the centroid for non-pollarded trees showed the opposite trend.

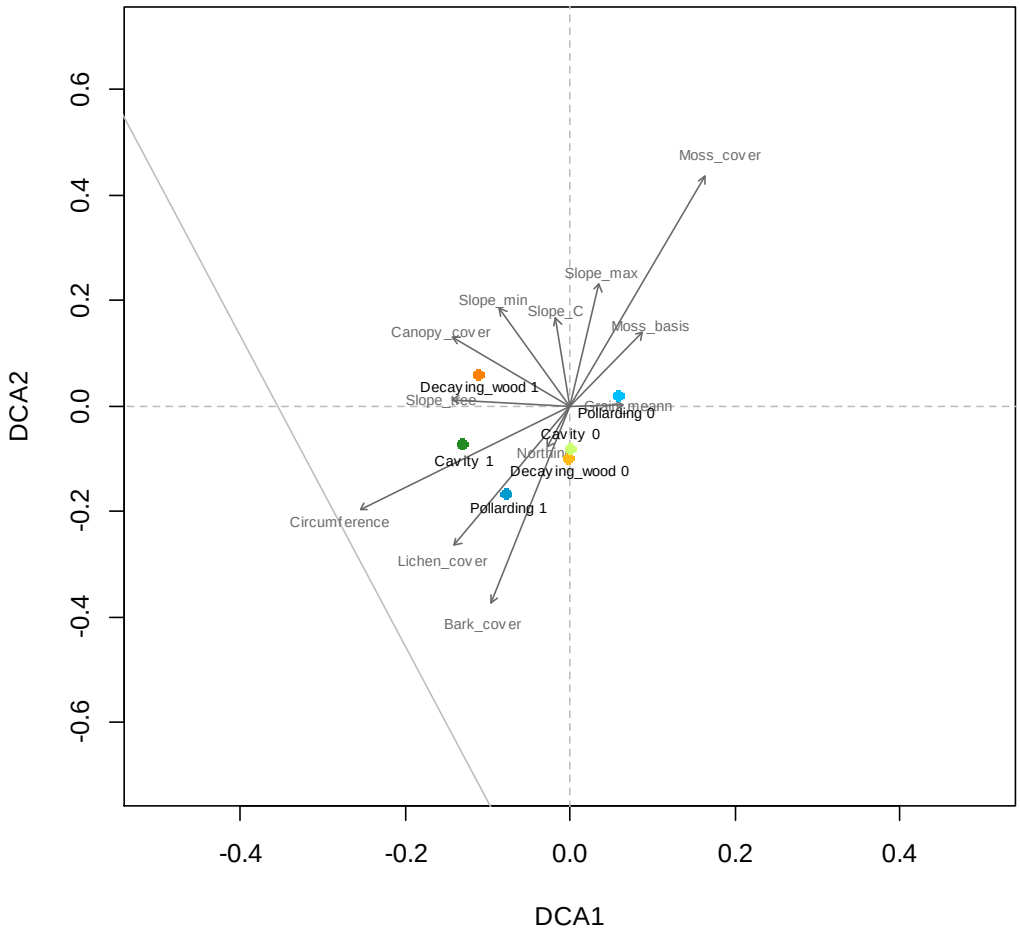



**FIGURE 13 SELECTED ENVIRONMENTAL VARIABLES FITTED TO THE DCA ORDINATION, AXES 1 AND 2. AXES ARE SCALED IN S.D. UNITS. CONTINUOUS VARIABLES ARE REPRESENTED BY VECTORS POINTING IN THE DIRECTION OF MAXIMUM INCREASE OF THE VARIABLE, CATEGORICAL VARIABLES ARE REPRESENTED BY THE CENTROID OF EACH FACTOR LEVEL. FACTOR-LEVEL 1 INDICATES PRESENCE AND LEVEL 0 INDICATES ABSENCE OF THE RESPECTIVE MICROHABITAT.**

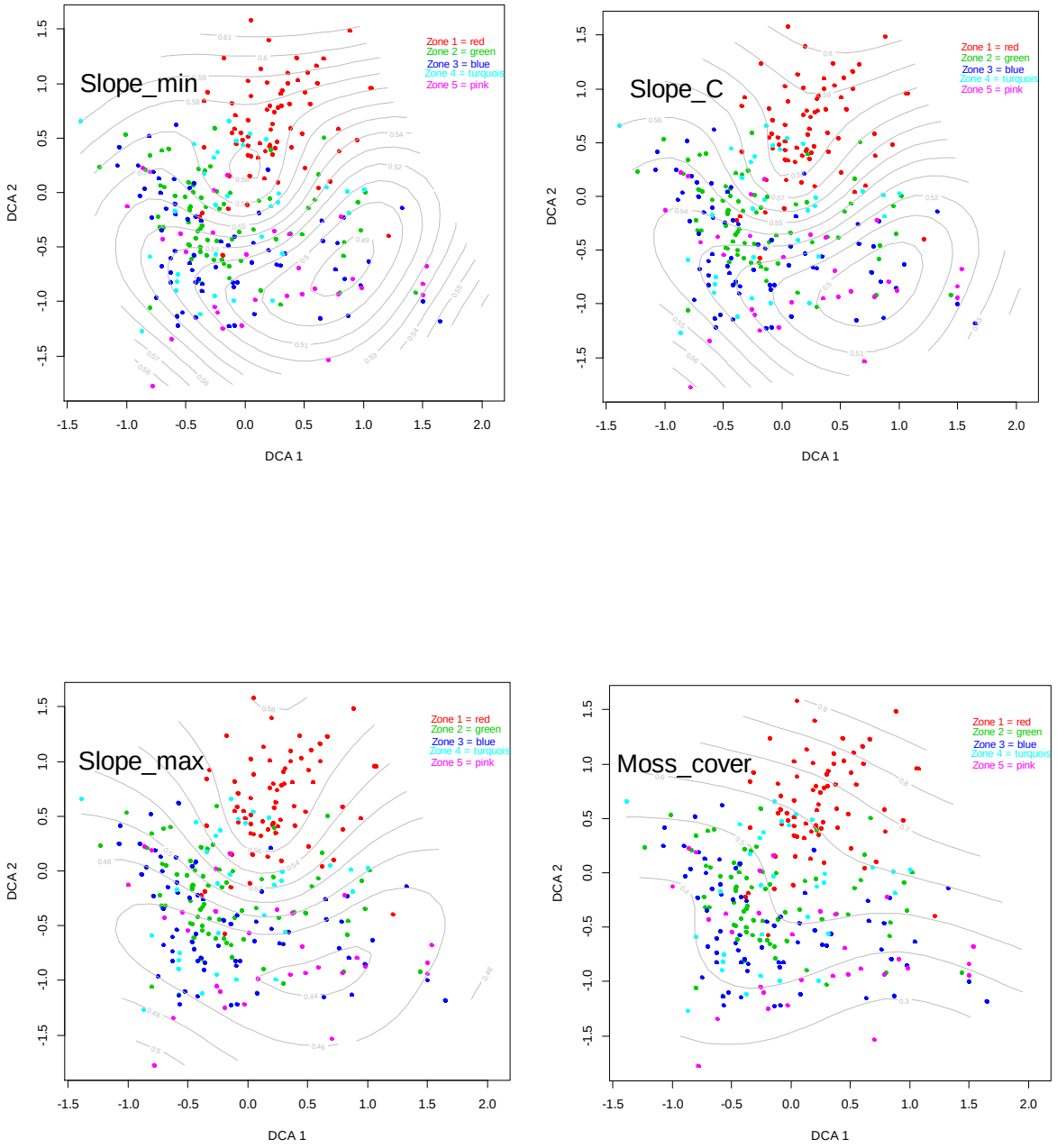



**FIGURE 14 SELECTED ENVIRONMENTAL VARIABLES FITTED TO THE DCA ORDINATION, AXES 1 AND 2. AXES ARE SCALED IN S.D. UNITS. CONTINUOUS VARIABLES ARE REPRESENTED BY CONTOUR LINES, SO THAT THE SPACING OF LINES INDICATES THE RATE OF INCREASE/DEACREASE OF THE VARIABLE IN QUESTION. AFFILIATION OF COU'S TO FACTOR LEVELS IN INDICATED BY A COLOUR.**

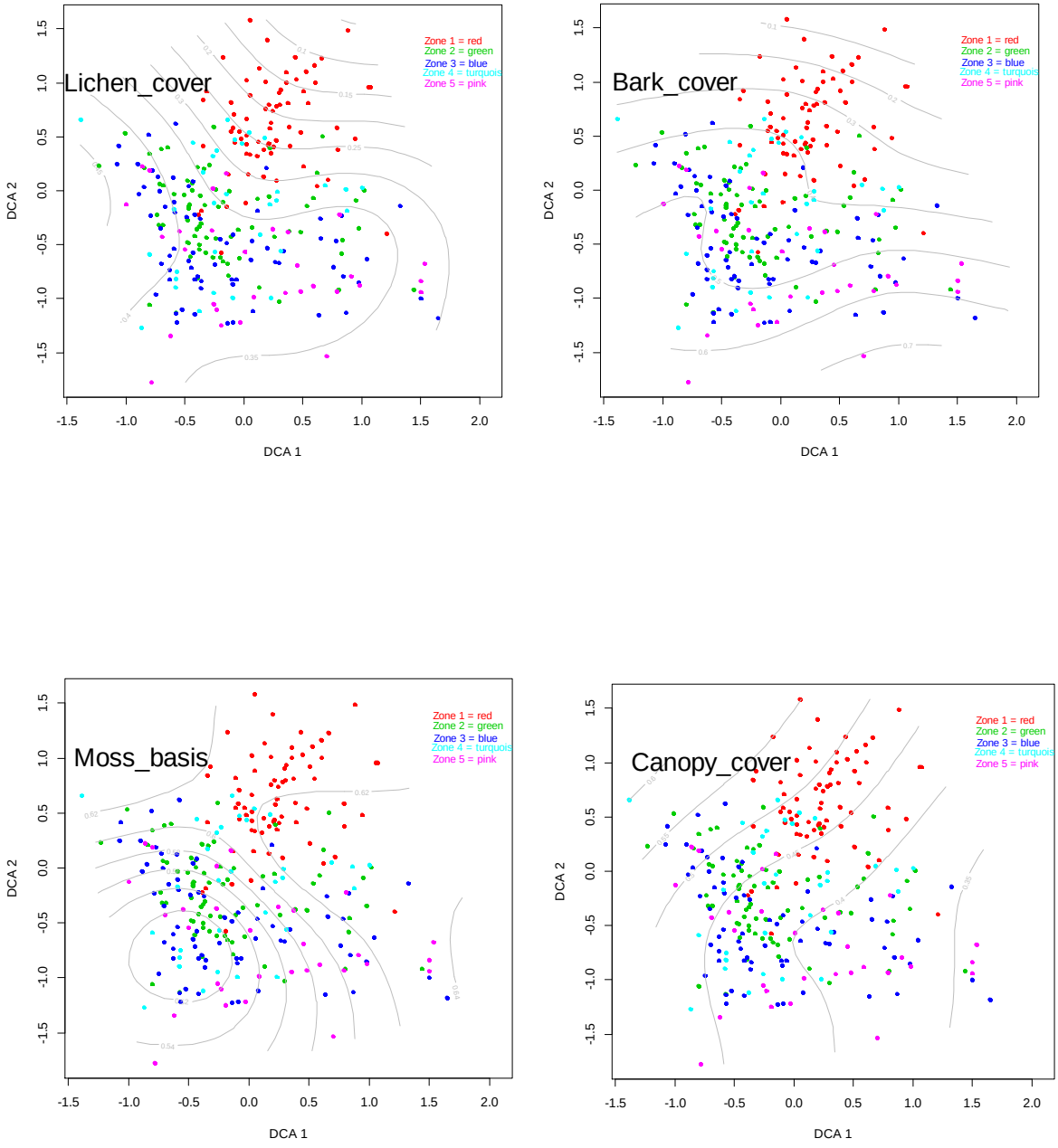



**FIGURE 15 SELECTED ENVIRONMENTAL VARIABLES FITTED TO THE DCA ORDINATION, AXES 1 AND 2. AXES ARE SCALED IN S.D. UNITS. CONTINUOUS VARIABLES ARE REPRESENTED BY CONTOUR LINES, SO THAT THE SPACING OF LINES INDICATES THE RATE OF INCREASE/DEACREASE OF THE VARIABLE IN QUESTION. AFFILIATION OF COU'S TO FACTOR LEVELS IN INDICATED BY A COLOUR.**

## SPATIAL STRUCTURE

The standardized semivariograms for environmental variables and DCA axes for the zonal and sectors COU matrices revealed the same semivariance patterns and hence only results for the zonal COU matrices are shown.

For most explanatory variables, the standardised semivariance did not vary systematically with distance class, indicating weak spatial structure or absence of spatial structure altogether. Four variables showed indications of spatial structure at fine scales. Circumference (Figure 16) and Canopy_cover (Figure 17) were spatially structured for lag-class 1 (up to a range of ca. $2^3$ = 8 m). The semivariance for Circumference levelled out with distances of 20 meters (lag class 4) which illustrates a spatial structure below this point and independence between pairs above (sill). The semivariance of Canopy_cover (see Figure 17) also revealed a spatial structure in lag class 1 (0-9 m), with the sill reached at about 14 meters. Moss_basis (Figure 18) showed a more irregular pattern, with the semivariance levelling off of at around a range of ca. $2^5$ = 32 m. This variable demonstrated a spatial structure in lag class 1 and 2, with distances of 0-9 meters and 9-14 meters, while the semivariance reached sill at 27 meters. The semivariance for Grind_mean (see Figure 19) also levelled out with distances of 27 meters (lag class 1) which illustrated a spatial structure below this point and the reach of (sill).

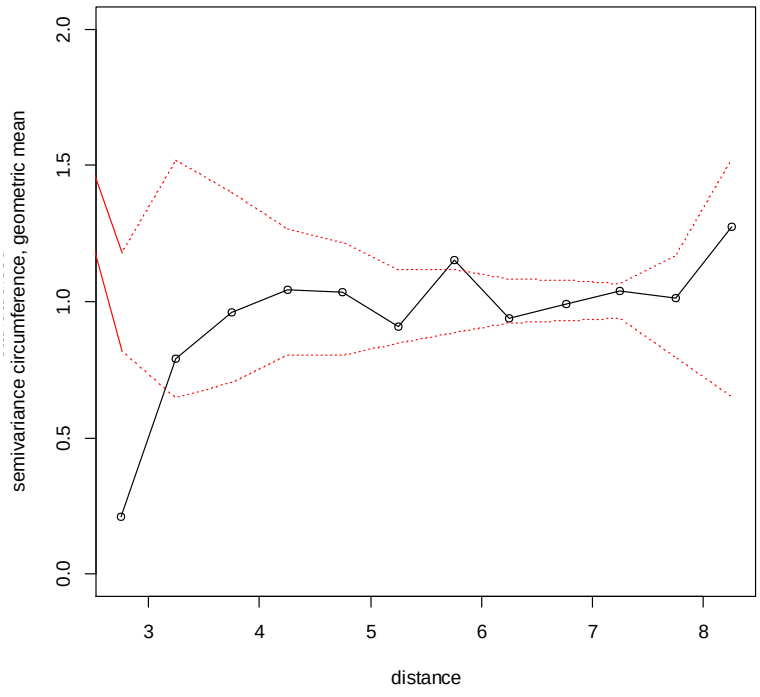



**FIGURE 16 STANDARDISED SEMIVARIOGRAM FOR CIRCUMFERENCE. DISTANCE IS MEASURED ON A $LOG_2$ SCALE. PUNCRUATED LINES REPRESENT ENVELOPE (95 % CONFIDENCE INTERVALL).**

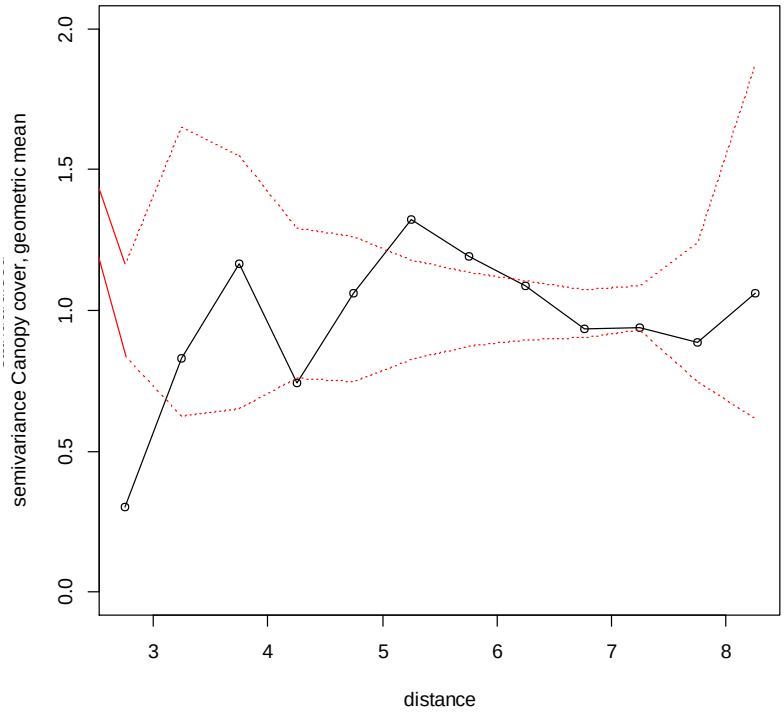



**FIGURE 17 SEMIVARIOGRAM FOR CANOPY_COVER, DISTANCE IS MEASURED IN A $LOG_2$ SCALE. PUNCRUATED LINES REPRESENT ENVELOPE (95 % CONFIDENCE INTERVALL).**

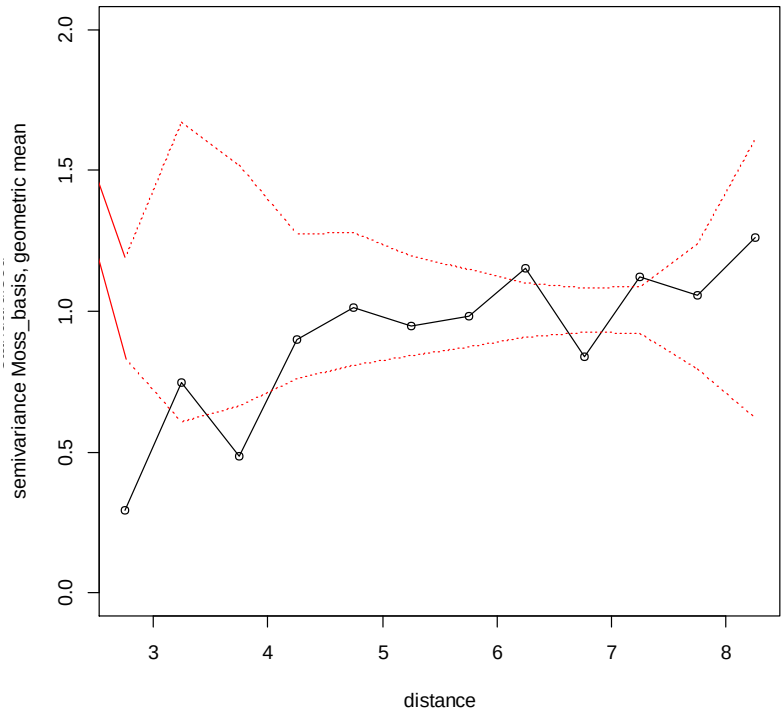



**FIGURE 18 SEMIVARIOGRAM FOR MOSS_BASIS, DISTANCE IS MEASURED IN A LOG2 SCALE PUNCRUATED LINES REPRESENT ENVELOPE (95 % CONFIDENCE INTERVALL).**

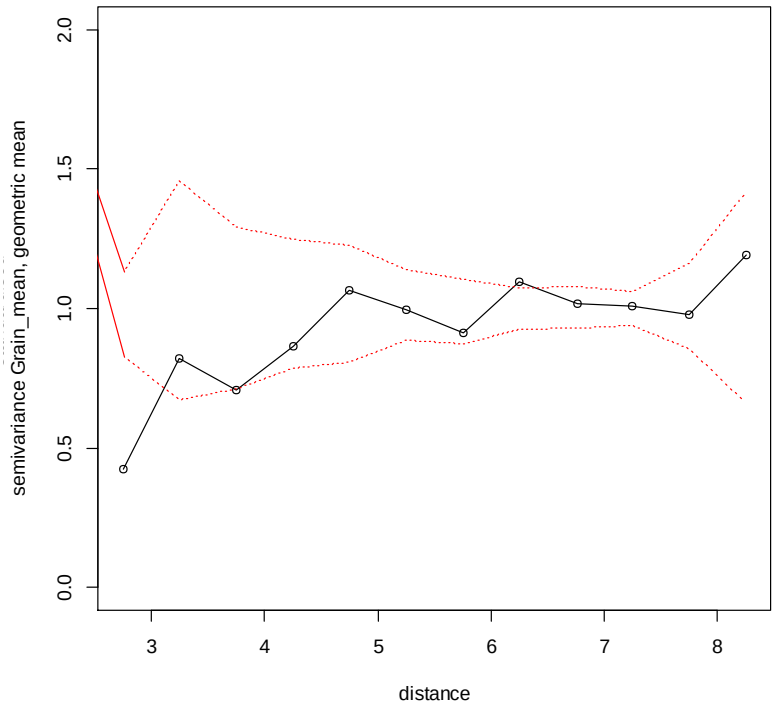



**FIGURE 19 SEMIVARIOGRAM FOR GRAIN_MEAN, DISTANCE IS MEASURED IN A $LOG_2$ SCALE. PUNCRUATED LINES REPRESENT ENVELOPE (95 % CONFIDENCE INTERVALL).**

## THE EFFECT ON POLLARDING ON THE SPECIES COMPOSITION

Pollarding explained 0.071 inertia units of a total inertia of 5.174 in the zonal COU data set in a CCA analysis. The fraction of variation explained (FVE) by the constrained axis was 1.4% of the total inertia. Pollarding contributed more to explaining variation in species composition than a random variable (Monte Carlo permutation test: p=0.001). After the variation due to tree size (as represented by the variable Circumference) was accounted for as a conditioning variable, pollarding explained 0.034 inertia units or 0.6% of the total inertia; significantly (p=0.011) more than expected by a random variable.

# DISCUSSION

## THE MAIN GRADIENT IN BRYOPHYTE SPECIES COMPOSITION

The DCA ordination analyses revealed one main gradient in bryophyte species composition that manifested itself on two different spatial scales, between and within trees. This gradient is related to both of DCA axes 1 and 2, and will be described as running from the upper right to the lower left corner of the two-dimensional DCA diagram in Fig. 12. On the scale of variation between trees, the main gradient described variation from trees with small diameter and high moss cover to trees with large diameter and lower moss cover. On the scale of variation within trees, the main gradient was related to tree height zones, running from the basis of the tree (zone 1) with high moss cover and low bark and lichen cover to higher height zones with decreasing moss cover and increasing bark and lichen cover. Parallel gradients in epiphytic species composition on stand level and within stand level was also found in studies by McCune and Antos (1981) and McCune (1993); a phenomenon they referred to as the "similar gradient hypothesis" because it is related to a gradient of variation in between trees of different ages and a vertical gradient within trees.

I will start my discussion of the main gradients by considering the contributions of different ecological factors to the main compositional gradients revealed by DCA ordination. Variation at the two different scales, at which variation along the gradient is expressed, will be discussed separately.

## ECOLOGICAL FACTORS MAKING UP COMPLEX GRADIENT UNDERLYING THE MAIN GRADIENT IN SPECIES COMPOSITION: VARIATION IN BRYOPHYTE COMPOSITION BETWEEN TREES

Previous studies have shown that trees with high diameter, which is a proxy for old tree age, host a richer epiphytic bryophyte flora due to changes of bark structure which is beneficial for a majority of species (Gustafsson and Eriksson 1995), increases microhabitat diversity (McGee and Kimmerer 2004), and prolongates colonization time (Snäll et al. 2003). The present study does, however, not confirm the pattern observed in these previous studies that bryophyte cover increases with increasing tree diameter. For instance, the GLM split-plot analyses showed that bryophyte cover (Moss_cover) was the most important variable explaining the variation along the main compositional gradient in the DCA ordination, but with decreasing bryophyte cover with increasing tree age, in contrast to the above-mentioned studies. However, although the PCA ordination indicated a negative association between bryophyte cover and tree circumference (arrows pointing in the same direction along the major axes), Kendall's tau calculated between the two variables themselves (se Appendix 2) indicated a weak

and non-significant (p=0.07) direct relationship, as shown in Figure 20. The non-significant relationship between circumference and bryophyte cover shows that these two variables increase and decrease more or less independently, suggesting that bryophyte cover does not decrease along the main gradient *as a result of* increasing tree age, but that high tree age and sites with reduced bryophyte cover tend to have similar species composition.

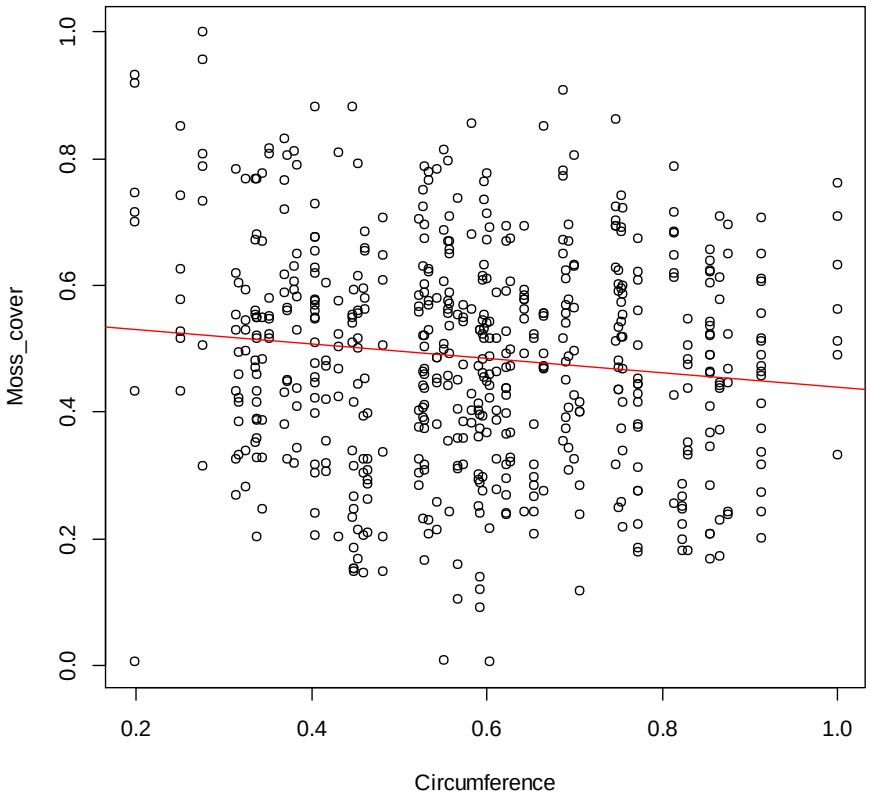



**FIGURE 20 CORRELATION BETWEEN MOSS_COVER AND CIRCUMFERENCE WITH REGRESSION LINE**

Furthermore, the apparent relationship between bryophyte cover and tree age along the main gradient in species composition may simply be an artifact of the zone-sector design (COUs) used in the present study, which gives heavier weight to the generally larger pollarded trees (represented by 20 COUs each, in five zones) than to non-pollarded trees (represented by 12 COUs). The centroids of zones 4 (pollarded crown) and 5 (pollarded branches), only present on pollarded trees, are placed in the lower part of the DCA axis 1 and 2, typical of large trees and trees with low bryophyte cover). Especially zone 5, but also to some degree zone 4, have lower bryophyte cover and higher lichen and bark cover than lower zones. This may therefore explain the opposite directions of tree circumference and moss cover vectors in the ordination diagram in Fig. 12. Representation of the large, pollarded trees with 5 zones of which

the 2–3 upper zones have low moss cover, makes an impression that larger trees have lower moss cover in general. Instead of a general decrease of bryophyte cover with increasing tree circumference, the results accord with an explanation that the vertical and horizontal distribution patterns of bryophytes along the stem change with tree age and with pollarding. The cutting of top branches drastically changes the structure of the upper part of stem, where lower moss cover results (Figure 12).

Bryophyte cover and the other cover variables are not *environmental* variables in the same way as *e.g*., slope and nothing, rather they describe characteristics of the bryophyte layer that, through co-variation with species composition, may be an expression of other impacting factors *e.g*., colonization time. Even though the differences between zones 1, 2 and 3 for pollarded and non-pollarded trees were shown to be small (Fig. 12), there was a general trend for the centroids of zones of pollarded trees to be placed towards the high circumference-low bryophyte cover end of the main gradient. This supports the explanation that bryophyte cover is not in general related to tree age in the study area. In a study of substrate type and forest age effects on bryophytes Perpetua et al. (2005) also found that most bryophyte species were not restricted to age classes, but rather restricted to a horizontal or vertical substrate types. Even though the findings in the present study show little or no difference between bryophyte cover for differently aged trees *as such*, inclusion of younger trees in the data set would most likely have revealed a difference: in the present study, only trees with circumference larger than 20 cm were included. Most likely, the main gradient in species composition starts with a colonization stage on small, young trees (with small circumference), from which moss cover increases until a stage is reached where further gains in bryophyte cover are balanced by age-dependent losses as the bark cramps and peels off and new microhabitats are created. My results suggest that this balance may be reached for ash already at tree ages where the diameter is 20 cm. The low bryophyte cover of pollard branches accords with this, since these branches are younger and of small circumference. The placement of zone 5 in Figure 12 separate from all other zones, characterised by high lichen and naked bark cover, and low bryophyte cover, to some extent may illustrate the species composition of younger stems. The fact that zone-5 COUs do not align on the end of the main gradient does, however, indicate that pollard braches may have a bryophyte flora distinctly different from that of young stems.

The GLM split-plot analyses show that circumference is the second most important variable for DCA axis 1 in explaining variation between trees, where its sign for Kendall's tau was negative (see Table 4) while bryophyte cover showed the opposite trend. This can be explained by the age-aspect of the tree's circumference (Heylen et al. 2005, Heylen and Hermy 2008, Márialigeti et al. 2009). Our results accord with the following explanation: The young trees with small circumference represent an early stage in the succession of epiphytic bryophyte species, with species that are good colonizers with good dispersal and establishment ability. The number of such species is low; there are fewer species on younger than on older trees (Hazell et al. 1998, Ingerpuu et al. 2007, Mežaka et al. 2008). The species that establish on young trees

grow and spread rapidly and trees obtain high bryophyte cover at an early age. High cover in young stands was, for example, observed by Heylen and Hermy (2008) for the epiphytic liverworts (*Frullanina dilatata, Metzgeria furcate* and *Radula complanata*). The decrease in cover of these species, all frequently found on the studied ash trees in Tungesvik, on old trees, indicates that older trees provided to less favorable substrates for them.

Vectors for the variables Moss_basis and Moss_cover point in the same direction in Figure 12, indicating that ground-living species 'climb' from the ground onto the lower basis of the tree. Weibull and Rydin (2005), who investigated bryophyte species richness on boulders in two deciduous forests in Sweden, one of which contained old pollarded trees, found that most of the bryophyte species that occurred on the boulders also occurred on the tree trunks and that rich-bark trees, especially *F. excelsior*, hosted an environment rich in bryophyte species, among others through enriched throughfall precipitation and litter deposited onto the boulders. The high bryophyte species richness and cover of the base at the tree trunks in the present study could therefore, at least partly, be due to a positive feedback effect where litter and leachates from the trees add to nutrient and species richness of the ground, from which the epigeous species enter tree bases and contribute to increasing bryophyte species richness on trees.

The GLM split-plot analyses show that the presence of exposed decaying wood explains a significant amount of the variation within trees for DCA axis 2, whereas Cavity was not significantly related to any of the axes (see Table 4 and 5). Figure 13 shows that the centroid of the variable Decaying_wood was projected on the positive side of the circumference vector and the negative side of the moss cover vector, illustrating that the frequency of microhabitats increases towards trees with larger diameter and that these microhabitats tend to have lower bryophyte cover than bark. When wood decays, old wood is exposed that does not have the rough texture of the outermost bark layer. Such microhabitats are likely to function as substrates for pioneer species, as exemplified by observations of *Mnium hornum* and *Tetraphis pellucida* on exposed decaying wood in the present study. Decaying wood is an important key biotope for several species and the presence of old trees in these deciduous forests may add to the area's bryophyte diversity by contributing to microhabitat diversity. Decaying wood was in this study only included as a presence/absence variable. Further studies of successions on microhabitats are needed.

## ECOLOGICAL FACTORS MAKING UP COMPLEX GRADIENT UNDERLYING THE MAIN GRADIENT IN SPECIES COMPOSITION: VARIATION IN BRYOPHYTE COMPOSITION WITHIN TREES

The GLM split-plot analysis showed that the largest fraction of variation explained by axis 2 were explained at the within-trees scale, and that the two most important variables accounting for variation at this scale were bryophyte cover and zones. This demonstrates the important vertical compositional gradient within trees, comprising variation from lower zones with high bryophyte cover to upper zones with lower bryophyte cover (and a corresponding variation in species composition). This is illustrated most clearly in the DCA plot with fitted environmental variables (Figure 12) and in the isoline diagrams (*e.g.,* Fig. 14), where zones 1 to 3 for both pollarded and non-pollarded trees replaced each other along the gradient from the upper right corner of the two-dimensional DCA diagram (high scores for both axes) to the lower left corner.

The PCA ordination of environmental variables shows that an increase in slope was correlated with an increase in bryophyte cover. The GLM split-plot analysis for DCA axis 2 shows trat the maximum slope measured in each COU (Slope_max) was the variable that explained the largest fraction of variation in species composition among all slope variables, followed by Slope_C and Slope_min. Slope_max represents the variation in inclination from vertical to horizontal plane at COU level. The vector of Slope_max points most closely in the direction of the bryophyte-cover vector (see Figure 12) and Figure 14 for Slope_max illustrates that this variable decreases rapidly from zone 1 towards the other zones. This rapid shift in slope between basis and stem shows that a major change in species composition takes place at this transition, with the change from a more horizontal to a vertical substrate. In a study on the effect of chemical and physical factors on epiphytes that live on ash and sessile oak (*Quercus petraea*), Bates (1992) found that the most important factor controlling the occurrence of epiphytes on tree trunks appeared to be the moisture of the bark surface. The vertical gradient on the trunk may be explained largely as a water availability gradient: with increasing height on the trunk, environments get drier due to greater wind speeds and turbulence and less influence by evaporation from the ground, Bates (1992) also found that more vertical stems had higher water-flow rates. Similar vertical patterns were also found by McCune (1993) who describes the lower part of the trunk as continuously wet and the upper part as frequently wet, but drying out rapidly. Another important factor that may contribute to the change in species distributions along the trunk is the bryophytes' ability to hold on to the surface. Bryophytes attach to substrates by tiny, single-cell rhizoids and differences in bryophyte rhizoids' ability to attach to a substrate may also contribute to explain the vertical pattering along the tree trunk (Glime 1987). The changing slope along the trunk, and the associated change in both water flow and the mosses' ability to hold on to the substrate, may therefore together explain the nonlinear distribution of the zones along the main gradient; zone 1 distinctly different from zones higher up on the trees (Fig. 12).

The placement of the zones along the main gradient in species composition can be explained both by the change in surface slope along the tree – zone 1 (basis), for pollarded as well as non-pollarded trees, occupy a position in the ordination diagram that can be projected onto the positive side of Slope_max (see Figure 12) – and by the elevation of the zones above ground. Zone 1 was particularly rich in bryophyte species, due to the mixture of epigeous and epiphytic species (Moe and Botnen 1997). The larger distance of zone 1 from all the other zones than between any other pair of zones is likely to be due to the upper zones' lack of epigeous species. There is a large group of species that may occur at the basis of the trunk, but that are unable to "climb" further up. The projection of zone 1 on the negative side of vectors for variables bark and lichen cover projecting from zone 1 also accords with these results and seem to reflect a general pattern (Bates 1992, McCune et al. 1997, Ruchty et al. 2001, Fritz 2009, Juriado et al. 2009) that bryophytes are able to photosynthesize and therefore to survive at lower light levels than lichens, while at the same time they require higher and more stable humidity levels (Fritz 2009).

For pollarded trees, zone 4 is the zone which is situated most closely to zone 1 along the main gradient. This may be surprising, given that zone 4 is physically separated from zone 1 on each tree. However, zone 4 shares with zone 1 high bryophyte cover and a more horizontal substrate than other zones (higher Slope_max). The typical spherical shape of zone 4 may make the substrate easier to colonize, and water may be kept for a longer time due to reduced water flow (McCune 1993). Zone 4 is, however, situated close to zone 2 along the gradient, reflecting that the two zones are typically dominated by the same species (*e.g., Hypnum cupressiforme, Isothecium alopecuroides and Homalothecium sericeum*). The similar species compositions of zones 2 and 4 may be due to similarity with respect to exposition to drought. The pollarded crown (zone 4) is likely to be much more exposed to drought spells than the basis. Own observations in the field shows that zone 4 is poor in species, also because it is not accessible for epigeous species by clonal growth, but has high moss cover. This pattern appears not to have been noted before, because earlier research on pollarded trees has not investigated the pollarded crown as a separate unit.

Zone 3 occupies the extreme position on the main gradient, both for pollarded and non-pollarded trees (Figure 12), indicating responses to higher exposure to drought and perhaps also higher probability for physical disturbances at higher elevations above the ground (Bates 1992), but also revealed a negative relationship to Slope_max which illustrate the zones negative inclination and thereby making it a more difficult substrate to hold on to.

The sectors, giving the position relative to the upper and under side of the trunk, showed pattern that accorded with that observed for the zones: the upper side of the tree (sector 1) is more similar in species composition to zone 1, while the underside (sector 3) takes the opposite position along the main gradient. This indicates that environmental conditions of sector 1 are more similar to those prevailing at the basis,

while conditions of sector 3 are more similar to high-elevation zones. The upper side of the stem resembles the basis in a more horizontal surface, while the overhang typical of the underside makes this substrate difficult for the bryophytes to hold on to, and prevents direct supply of water.

## EXISTENCE OF A SECONDARY GRADIENT IN SPECIES COMPOSITION RELATED TO CANOPY COVER?

Canopy cover was recorded as a proxy for available light. Figure 12 illustrates that this variable has a pattern unlike the other variables in the ordination diagram, pointing in a direction perpendicular to the main gradient and increasing with increasing DCA axis 2 scores. The positive relationship with DCA axis 2, shared with bryophyte cover, may indicate that decreasing canopy to some degree has a similar effect on the species composition as the variation from basis towards higher zones, resulting in decrease of epigeous and basis-bound species (Márialigeti al. 2009). According to the GLM split–plot analysis, canopy cover was the only variable that was significantly related to DCA axis 2 on the between-trees scale. However the relationship was not strong. Nevertheless, the direction of the canopy cover vector in the DCA ordination may indicate existence of a second gradient in species composition which is independent of the main gradient, and which describes variation at the between-tree scale. This interpretation is, however, tentative and requires more detailed examination.

## POLLARDING

The CCA test of the effect of pollarding on the epiphytic bryophyte species composition on ashes in Tungesvik shows that the fraction of variation explained (FVE) by the binary pollarding variable is only 1.4 %. This result is, however, likely to be an underestimate of the 'real' variation explained, because the FVE is inflated by being calculated by use of the total intertia, which also includes 'variation' due to lack of fit of data to the model, represented by polynomial distortion axes (Økland 1999). The 1.4 % of the total inertia explained by pollarding was significantly higher than expected of a random variable. In the present study area, Tungesvik, pollarding ceased several decades ago, and the investigated pollarded trees are of old age, not harvested for many decades. When circumference is included as a conditioning variable in the CCA, pollarding was still significant (0.6 % of the total interia; p=0.011), meaning that pollarding still explains significantly more variation than a random variable, even the effect of pollarded trees being larger than non-pollarded trees has been accounted for. This emphasises the importance of tree circumference for the species composition. Low importance of pollarding *in itself* is also indicated by the GLM split-plot analysis, ranking circumference as the second most important variable explaining the total variation along DCA axis 1 while pollarding was ranked as the ninth most important variable explaining the total variation along DCA axis 2.

The DCA diagram with fitted variables (see Figure 12) illustrates a small, but still consistent difference between pollarded and non-pollarded trees for corresponding zones of pollarded trees to obtain slightly lower DCA axis 1 and 2 scores than non-pollarded trees. This indicates a tendency of pollarded trees for a species composition indicative of higher tree circumference, lower bryophyte cover and an increase in bark and lichen cover and thereby placing the pollarded trees at a late successional phase representing trees of old age.

Several studies have pointed to high importance of pollarding for the epiphytic vegetation, mediated by characteristics like reduced canopy cover, tree longlivety and water conservation through increasing roughness of the bark (*e.g.,* Austad and Skogen 1988, Austad and Skogen 1990, Moe and Botnen 2000). None of these studies have, however, investigated differences between pollarded and non-pollarded trees explicitly and therefore cannot separate between effects of age in itself and pollarding. In the present study pollarding, tended to have similar effects on the bryophyte species composition as reduced bryophyte cover, even on the basis of the tree (Figure 12). If this trend in general holds true for pollarded trees, or if it is just a characteristic of pollarded trees at Tungesvik, is not yet known. Further investigations into these subtle differences are therefore needed. However, my study also shows that most of the effect of pollarding is jointly explained with tree diameter and leaves very little variation to be explained by pollarding *as such*. A complicating factor for the assessment of effects of pollarding is that the study area has not been actively pollarded for several decades. It is not unlikely that well-maintained and abandoned pollards provide different growth conditions for bryophytes; *e.g.*, that actively pollarded trees have a smaller, more open canopy. This may influence the bryophyte cover positively (by enhancing light availability) or negatively (but increasing the exposure to desiccation). In order to investigate the general effect of pollarding, also the variation between different tree species and local differences must be taken into account: pollarding may not have the same effect on epiphytic species responses in all areas. Likewise, the different techniques of pollarding (Austad and Skogen 1988) may result in different responses of different species, but detailed knowledge of this is presently lacking. Concerns regarding the loss of biodiversity of epiphytic bryophytes in both old-growth forests and forests of different ages (Perpetua et al. 2005) therefore motivate further investigations to reveal the major factors of importance for variation in epiphytic bryophyte species composition.

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**A**ppendix 1

| **Bryophyte species** | **Abbreviations** | **Norwegian name** |
|---|---|---|
| Amblystegium serpens | AMBLser | Trådkrypmose |
| Atrichum undulatum | ATRIund | Stortaggmose |
| Barbilophozia barbata | BARBbar | Skogskjeggmose |
| Barbilophozia lycopodioides | BARBlyc | Gåsefotskjeggmose |
| Brachythecium populeum | BRACpop | Ospelundmose |
| Brachythecium rutabulum | BRACrut | Storlundmose |
| Bryum capillare | BRYUcap | Skruevrangmose |
| Bryum moravicum | BRYUmor | Trådskruevrangmose |
| Chiloscyphus polyanthos | CHILpol | Bekkeblonde |
| Climacium dendroides | CLIMden | Palmemose |
| Ctenidium molluscum | CTENmol | Kammose |
| Dicranum majus | DICRmaj | Blanksigd |
| Dicranum scoparium | DIRCsco | Ribbesigd |
| Dicranum fuscescens | DIRCfus | Bergsigd |
| Eurhynchium striatum | EURHstr | Kystmoldmose |
| Frullania dilatata | FRULdil | Hjelmblæremose |
| Frullania tamarisci | FRULtam | Matteblæremose |
| Grimmia hartmanii | GRIMhar | Sigdknausing |
| Homalia trichomanoides | HOMAtri | Glansmose |
| Homalothecium sericeum | HOMAseri | Krypsilkemose |
| Hylocomiastrum pyrenaicum | HYLOpyr | Seterhusmose |
| Hylocomium splendens | HYLOspl | Etasjemose |
| Hypnum cupressiforme | HYPNcup | Matteflette |
| Isothecium alopecuroides | ISOTalo | Rottehalemose |
| Isothecium myosuroides | ISOTmyo | Musehalemose |
| Lejeunea cavifolia | LEJEcav | Glansperlemose |
| Leucodon sciuroides | LEUCsci | Ekornmose |
| Loeskeobryum brevirostre | LOESbre | Kystmose |
| Metzgeria conjugata | METZcon | Kystband |
| Metzgeria fruticulosa | METZfur | Blåband |
| Mnium hornum | MNIUhor | Kysttornemose |
| Neckera complanata | NECKcom | Flatfellmose |
| Neckera crispa | NECKcri | Krusfellmose |
| Orthotrichum affine | ORTHaff | Klokkebustehette |
| Orthotrichum lyellii | ORTHlye | Kystbustehette |
| Orthotrichum pallens | ORTHpal | Gulltannbustehette |
| Orthotrichum pulchellum | ORTHpul | Vribustehette |

| | | |
|---|---|---|
| Orthotrichum rupestre | ORTHrup | Faksbustehette |
| Orthotrichum speciosum | ORTHspe | Duskbustehette |
| Orthotrichum stramineum | ORTHstra | Bleikbustehette |
| Orthotrichum striatum | ORTHstri | Tønnebustehette |
| Plagiochila asplenioides | PLAGIOCasp | Prakthinnemose |
| Plagiochila porelloides | PLAGOICpor | Berghinnemose |
| Plagiomnium affine | PLAGIOMaff | Skogfagermose |
| Plagiomnium cuspidatum | PLAGIOMcus | Broddfagermose |
| Plagiomnium ellipticum | PLAGIOMell | Sumpfagermose |
| Plagiomnium medium | PLAGIOMmed | Krattfagermose |
| Plagiomnium undulatum | PLAGIMund | Krusfagermose |
| Plagiothecium succulentum | PLAGIOTsuc | |
| Plagiothecium undulatum | PLAGIOTund | Kystjamnemose |
| Platydictya jungermannioides | PLATjun | Hårmose |
| Pleurozium schreberi | PLEUsch | Furumose |
| Pohlia cruda | POHcru | Opalnikke |
| Pseudoleskeella nervosa | PSEUner | Broddtråklemose |
| Pterigynandrum filiforme | PTRIfil | Reipmose |
| Pterogonium gracile | PTERgra | Kveilmose |
| Ptilium crista-castrensis | PTILcri-cas | Fjørmose |
| Racomitrium affine | RACOaff | Kollegråmose |
| Radula complanata | RADUcom | Krinsflatmose |
| Rhizomnium punctatum | RHIZpun | Bekkerundmose |
| Rhytidiadelphus loreus | RHYTlor | Kystkransmose |
| Rhytidiadelphus triquetrus | RHYTtri | Storkransmose |
| Scapania aspera | SCAPasp | Vortetvebladmose |
| Scapania gracilis | SCAPgra | Kysttvebladmose |
| Scapania nemorea | SCAPnem | Fjordtvebladmos |
| Tetraphis pellucida | TETRpel | Firtannmose |
| Thamnobryum alopecurum | THAMalo | Revemose |
| Thuidium tamariscinum | THUItam | Stortujamose |
| Ulota coarctata | ULOTcoa | Pløsegullhette |
| Ulota crispa | ULOTcri | Krusgullhette |
| Ulota drummondii | ULOTdru | Snutegullhette |
| Zygodon conoideus | ZYGOcon | Askkjølmose |
| Zygodon rupestris | ZYGOrup | Trådkjølmose |

Appendix 2

| Variable 1 | Variable 2 | Summary statistics of transformed variable | | Correlation coefficient |
|---|---|---|---|---|
| | | Z-value | p-value | (τ) |
| **Circumference** | **Slope_C** | **5.054** | **4.33E-07** | **0.1435475** |
| **Circumference** | **Slope_min** | **4.618** | **3.88E-06** | **0.1317267** |
| **Circumference** | **Slope_max** | **4.2983** | **1.72E-05** | **0.1219844** |
| **Circumference** | **Slope_tree** | **2.2674** | **2.34E-02** | **0.06512683** |
| **Circumference** | **Canopy_cover** | **3.612** | **0.0003038** | **0.1025445** |
| Circumference | Moss_basis | -1.3241 | 0.1855 | -0.03876874 |
| Circumference | Grain_mean | -0.3683 | 0.7127 | -0.01083993 |
| Circumference | Moss_cover | -1.8289 | 0.06741 | -0.05182508 |
| **Circumference** | **Lichen_cover** | **2.8774** | **0.004009** | **0.08191373** |
| Circumference | Bark_cover | 0.7591 | 0.4478 | 0.02150845 |
| Circumference | Northing | 0.2422 | 0.8086 | 0.006998025 |
| | | | | |
| **Slope_C** | **Circumference** | **5.054** | **4.33E-07** | **0.1435475** |
| **Slope_C** | **Slope_min** | **22.7503** | **2.20E-16** | **0.6462064** |
| **Slope_C** | **Slope_max** | **24.7751** | **2.20E-16** | **0.7001332** |
| **Slope_C** | **Slope_tree** | **5.6077** | **2.05E-08** | **0.1603902** |
| **Slope_C** | Canopy_cover | -1.0049 | 0.3149 | -0.02840902 |
| Slope_C | Moss_basis | 0.0923 | 0.9265 | 0.002689848 |
| Slope_C | Grain_mean | -0.4527 | 0.6508 | -0.01326868 |
| **Slope_C** | **Moss_cover** | **7.4488** | **9.42E-14** | **0.2101802** |
| **Slope_C** | **Lichen_cover** | **-5.0606** | **4.18E-07** | **-0.143455** |
| **Slope_C** | **Bark_cover** | **-5.8005** | **6.61E-09** | **-0.1636605** |
| Slope_C | Northing | 0.7379 | 0.4606 | 0.02122929 |
| | | | | |
| **Slope_min** | **Circumference** | **-0.02157808** | **3.88E-06** | **0.1317267** |
| **Slope_min** | **Slope_C** | **22.7503** | **2.20E-16** | **0.6462064** |
| **Slope_min** | **Slope_max** | **20.3774** | **2.20E-16** | **0.5783337** |
| **Slope_min** | **Slope_tree** | **4.1551** | **3.25E-05** | **0.1193549** |
| Slope_min | Canopy_cover | 0.0124 | 0.9901 | 0.000352971 |
| Slope_min | Moss_basis | 1.695 | 0.09007 | 0.04963295 |
| Slope_min | Grain_mean | -1.534 | 0.125 | -0.04515643 |
| **Slope_min** | **Moss_cover** | **5.3191** | **1.04E-07** | **0.150732** |
| **Slope_min** | **Lichen_cover** | **-4.4983** | **6.85E-06** | **-0.1280657** |
| **Slope_min** | **Bark_cover** | **-3.7997** | **0.0001449** | **-0.1076691** |
| Slope_min | Northing | 0.2545 | 0.7991 | 0.007353578 |
| | | | | |
| **Slope_max** | **Circumference** | **6.8012** | **1.04E-11** | **0.1932** |
| **Slope_max** | **Slope_C** | **24.0131** | **2.20E-16** | **0.7001332** |

| | | | | |
|---|---|---|---|---|
| **Slope_max** | **Slope_min** | **20.3774** | **2.20E-16** | **0.5783337** |
| **Slope_max** | **Slope_tree** | **3.9103** | **9.22E-05** | **0.1117511** |
| Slope_max | Canopy_cover | -0.4088 | 0.6827 | -0.01154714 |
| Slope_max | Moss_basis | 0.3374 | 0.7358 | 0.009828523 |
| Slope_max | Grain_mean | -0.0494 | 0.9606 | -0.001447473 |
| **Slope_max** | **Moss_cover** | **8.3259** | **2.20E-16** | **0.2347368** |
| **Slope_max** | **Lichen_cover** | **-5.7821** | **7.38E-09** | **-0.1637758** |
| **Slope_max** | **Bark_cover** | **-6.3215** | **2.59E-10** | **-0.178213** |
| Slope_max | Northing | -0.1384 | 0.8899 | -0.003979947 |
| | | | | |
| **Slope_tree** | **Circumference** | **2.2674** | **2.34E-02** | **0.06512683** |
| **Slope_tree** | **Slope_C** | **5.6077** | **2.05E-08** | **0.1603902** |
| **Slope_tree** | **Slope_min** | **4.1551** | **3.25E-05** | **0.1193549** |
| **Slope_tree** | **Slope_max** | **3.9103** | **9.22E-05** | **0.1117511** |
| **Slope_tree** | Canopy_cover | 0.1475 | 0.8828 | 0.004215441 |
| **Slope_tree** | Moss_basis | -2.3798 | 0.01732 | -0.07016798 |
| **Slope_tree** | **Grain_mean** | **-3.9458** | **7.95E-05** | **-0.1169645** |
| Slope_tree | Moss_cover | 0.8267 | 4.08E-01 | 0.02359045 |
| Slope_tree | Lichen_cover | 0.6068 | 5.44E-01 | 0.01739654 |
| Slope_tree | Bark_cover | -0.86 | 3.90E-01 | -0.02453922 |
| **Slope_tree** | Northing | -0.6445 | 0.5192 | -0.01875321 |
| | | | | |
| **Canopy_cover** | **Circumference** | **3.612** | **3.04E-04** | **0.1025445** |
| Canopy_cover | Slope_C | -1.0049 | 3.15E-01 | -0.02840902 |
| Canopy_cover | Slope_min | 0.0124 | 9.90E-01 | 0.000352971 |
| Canopy_cover | Slope_max | -0.4088 | 6.83E-01 | -0.01154714 |
| Canopy_cover | Slope_tree | 0.1475 | 8.83E-01 | 0.004215441 |
| **Canopy_cover** | **Moss_basis** | **2.8265** | **0.004706** | **0.08237142** |
| Canopy_cover | Grain_mean | 1.9448 | 0.0518 | 0.05697876 |
| Canopy_cover | Moss_cover | -1.4023 | 1.61E-01 | -0.03955117 |
| Canopy_cover | Lichen_cover | 0.6882 | 0.4913 | 0.01949897 |
| Canopy_cover | Bark_cover | 1.0852 | 0.2778 | 0.03060483 |
| Canopy_cover | Northing | 1.0809 | 0.2797 | 0.03108304 |
| | | | | |
| Moss_basis | Circumference | -1.3241 | 1.86E-01 | -0.03876874 |
| Moss_basis | Slope_C | 0.0923 | 9.27E-01 | 0.002689848 |
| Moss_basis | Slope_min | 0.3374 | 7.36E-01 | 0.009828523 |
| Moss_basis | Slope_max | -0.1982 | 0.8429 | -0.0057 |
| **Moss_basis** | **Slope_tree** | **-2.3798** | **1.73E-02** | **-0.07016798** |
| **Moss_basis** | **Canopy_cover** | **2.8265** | **0.004706** | **0.08237142** |
| Moss_basis | Grain_mean | 1.6992 | 0.08929 | -0.05134416 |
| Moss_basis | Moss_cover | 1.4667 | 1.43E-01 | 0.04266251 |
| Moss_basis | Lichen_cover | -1.2536 | 0.21 | -0.03663302 |
| Moss_basis | Bark_cover | -0.6393 | 0.5226 | -0.0185947 |
| Moss_basis | Northing | -0.605 | 0.5452 | -0.01794364 |

| | | | | |
|---|---|---|---|---|
| Grain_mean | Circumference | -0.3683 | 7.13E-01 | -0.01083993 |
| Grain_mean | Slope_C | -0.4527 | 6.51E-01 | -0.01326868 |
| Grain_mean | Slope_min | -1.534 | 1.25E-01 | -0.04515643 |
| Grain_mean | Slope_max | -0.0494 | 9.61E-01 | -0.001447473 |
| **Grain_mean** | **Slope_tree** | **-3.9458** | **7.95E-05** | **-0.1169645** |
| Grain_mean | Canopy_cover | 1.9448 | 0.0518 | 0.05697876 |
| Grain_mean | Moss_basis | -1.6992 | 8.93E-02 | -0.05134416 |
| Grain_mean | Moss_cover | -0.1116 | 0.9111 | -0.003264902 |
| Grain_mean | Lichen_cover | 1.579 | 1.14E-01 | 0.04638982 |
| Grain_mean | Bark_cover | -0.4958 | 0.62 | -0.01449727 |
| Grain_mean | Northing | -0.8206 | 0.4119 | -0.02446739 |